ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Herausgeber/Editor

Deutsche Gesellschaft für Säugetierkunde

Schriftleitung/Editorial Office

D. Kruska, Kiel – P. Langer, Giessen

GUSTAV FISCHER

Volume 62

1997

Wissenschaftliche Originalarbeiten

Wissenschaftliche Kurzmitteilungen

Printed in Germany

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Indexed in Current Contents ®Agriculture, Biology & Environmental Sciences; Biological Abstracts; *BIOSIS* database

GUSTAV FISCHER

ISSN 0044-3468
Z. Säugetierkunde
Jena · 62(1997)1 · S. 1-64
Februar 1997

1
1997

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **62** (1997) 1–11

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Jagdaktivität von Fledermäusen an Bächen und Teichen

Von A. ZAHN und SANDRA MAIER

Zoologisches Institut der Universität München, München

Eingang des Ms. 15. 01. 1996
Annahme des Ms. 18. 09. 1996

Abstract

Hunting activity of bats at streams and ponds

Hunting activity of bats was studied at different types of streams and ponds in an area of 20 km^2 in size in south-eastern Bavaria from May to October 1993. We measured flight activity with help of bat detectors and used mist nets to catch bats. *Nyctalus noctula, Pipistrellus pipistrellus, Myotis myotis, Myotis emarginatus, Myotis mystacinus, Myotis daubentoni,* and *Myotis nattereri* were found during the period of the study. Additionally *Myotis brandti, Myotis bechsteini, Eptesicus serotinus, Plecotus auritus, Barbastella barbastellus,* and *Rhinolophus hipposideros* are known to be present in the area.
The bat activity was higher at streams and ponds situated in forests or lined by trees and bushes than at waters without surrounding high vegetation. Moreover, few bats were heard at small streams were branches left little space ("flight pass") over the water. Generally, bat activity was higher at ponds than at streams.

Wind shelter and insect density seemed to be of main importance for the quality of a foraging habiat.

Einleitung

Alle heimschen Fledermausarten stehen auf der Roten Liste gefährdeter Tierarten Deutschlands und Maßnahmen zu ihrem Schutz werden in vielen Publikationen vorgeschlagen (z. B. KLAWITTER 1988; MAYWALD und POTT 1988; RICHARZ 1986; RICHARZ und LIMBRUNNER 1992; SCHOBER und GRIMBERGER 1987). Meist steht dabei der Quartierschutz im Vordergrund, da hier die Probleme besonders augenfällig sind (Renovierungen) und viele Maßnahmen leicht umgesetzt werden können.

Für den Rückgang vieler Fledermausarten wird jedoch auch die Abnahme nahrungsreicher Jagdbiotope diskutiert (MAYWALD und POTT 1988; NAGEL und RICHARZ 1994; RICHARZ 1994). Im Zuge der Landschaftsplanung stellt sich daher oft die Frage, welche Jagdlebensräume für Fledermäuse besonders bedeutend sind.

Zwar wurden das Jagdverhalten und die Jagdbiotope einzelner Fledermausarten untersucht (z. B. AUDET 1990; DEGN 1983; KALKO und BRAUN 1991; KRONWITTER 1988; KRULL et al. 1991; NYHOLM 1965; RACHWALD 1992; RACEY und SWIFT 1985; RIEGER et al. 1990; 1992; TAAKE 1984), doch gibt es nur wenige Arbeiten, die in einem Landschaftsraum mit bekannter Fledermausfauna die Jagdaktivität in bestimmten Biotoptypen erfassen und vergleichen.

Gerade über Gewässer fehlen entsprechende Studien, obwohl an ihnen viele Fledermausarten angetroffen werden. Nach HELMER und LIMPENS (1991), LIMPENS und KAPTEYN (1991) sowie RIEGER et al. (1990) nützen Fledermäuse lineare Landschaftsstrukturen, zu denen auch Fließgewässer zählen, besonders als Flugrouten zu den Hauptjagdgebieten. WALSH

und Mayle (1991) sowie Taake (1992) verglichen Waldgewässer. Freilandgewässer blieben jedoch unberücksichtigt. Nyholm (1965), Racey und Swift (1985) und Taake (1984) weisen auf die Bedeutung gewässerreicher Lebensräume für verschiedene Arten hin, gehen aber nur am Rande auf strukturelle Merkmale oder die Bevorzugung bestimmter Teilflächen ein. In der vorliegenden Arbeit wurde die Jagdaktivität von Fledermäusen an unterschiedlichen Fließ- und Stillgewässern im Wald und im Freiland vergleichend untersucht.

Material und Methode

Untersuchungsgebiet und Artenspektum

Das ca. 20 km^2 große Untersuchungsgebiet befindet sich etwa 60 km südöstlich von München am südwestlichen Rand des Rosenheimer Beckens (Inn-Chiemsee-Hügelland). Die Höhe des Gebietes variiert von 450 bis 750 m über NN. Klimatisch ist das Rosenheimer Becken aufgrund der im Vergleich zum Umland geringen Meereshöhe und aufgrund von warmen Fallwinden im Einflußbereich der Alpen begünstigt. Die Landschaft ist kleinräumig strukturiert und geprägt von Grünland, Obstwiesen und Mischwäldern. Das Gebiet wird von vielen Wildbächen durchzogen. Ein Großteil der zahlreichen Teiche wird zur Fischzucht genutzt.

Folgende Fledermausarten wurden nach Richarz (1986), Richarz et al. (1989) sowie Zahn und Krüger-Barvels (1996) im Untersuchungsgebiet nachgewiesen (bei mit * markierten Arten wurden Kolonien festgestellt, so daß mit ihrem Auftreten im Gebiet sicher zu rechnen war): Kleine Hufeisennase (*Rhinolophus hipposideros*), Großes Mausohr (*Myotis myotis*)*, Bechsteinfledermaus (*Myotis bechsteini*), Wimperfledermaus (*Myotis emarginatus*)*, Fransenfledermaus (*Myotis nattereri*), Große Bartfledermaus (*Myotis brandti*), Kleine Bartfledermaus (*Myotis mystacinus*)*, Wasserfledermaus (*Myotis daubentoni*), Braunes Langohr (*Plecotus auritus*)*, Mopsfledermaus (*Barbastella barbastellus*)*, Großer Abendsegler (*Nyctalus noctula*), Zwergfledermaus (*Pipistrellus pipistrellus*)* und Breitflügelfledermaus (*Eptesicus serotinus*).

Datenerhebung

27 Untersuchungsflächen wurden an 15 Still- und 7 Fließgewässern ausgewählt. Während jedes Stillgewässer eine solche „Probestelle“ bildete, befanden sich an den Fließgewässern bis zu 5 Untersuchungsflächen (Mindestabstand 500 m). Alle Flächen lagen in der Nähe von Siedlungen mit bekannten Fledermauskolonien (< ca. 2 km). An den Probestellen wurden folgende Merkmale festgehalten:

Umgebung: Unterschieden wurde zwischen Gewässern im Wald (ringsum von einem mindestens 10 m breiten Waldstreifen umgeben) und solchen im Freiland (dazu zählten auch Gewässer am Waldrand)

Gehölzvegetation am Ufer: Bei Stillgewässern wurde die gehölzbestandene Uferlänge (in % der Gesamtuferlänge) ermittelt. Bei Bächen wurde unterschieden zwischen (a) Probestellen mit allenfalls spärlicher Gehölzvegetation (Abstand zwischen den Gehölzen mindestens 5 m und (b) Uferstellen mit dichtem Gehölzbewuchs (Abstand zwischen den Gehölzen unter 2 m).

Fließgeschwindigkeit: (subjektive Einteilung in gering, mittel und hoch)

Gewässergüte der Fließgewässer: Methode nach Baur (1980): Güteklassen I (unbelastet) bis II–III (kritisch belastet)

Fischbesatz der Stillgewässer (mit oder ohne Zufütterung)

„Vernetzung“ der Stillgewässer mit anderen potentiell für Fledermäuse wichtigen Landschaftselementen (Wälder, Siedlungen) durch Hecken, Baumreihen usw. vorhanden (ja/nein)

Von Anfang Mai bis Mitte Oktober wurde die Jagdaktivität der Fledermäuse in 75 Nächten erfaßt. Die Datenaufnahme begann bei Sonnenuntergang und wurde ca. 4 Stunden danach beendet. In einer Nacht wurden jeweils 15 Untersuchungsflächen begangen. Um alle Standorte zu unterschiedlichen Zeiten zu erfassen, wurde jeweils an einem anderen Gewässer mit der Datenerhebung begonnen. Die Verweildauer an einer Untersuchungsstelle betrug 10 Minuten. Während dieser Zeit wurde mit Hilfe eines Mini-QMC-Batdetektors die Jagdaktivität registriert. Einmal pro Monat wurde die Datenaufnahme auf die 2. Nachthälfte verlegt und 5 Stunden nach Sonnenuntergang begonnen.

Um die vorliegenden Ergebnisse mit anderen Arbeiten, die im selben Gebiet durchgeführt wurden (Schminke unpubl.; Zahn und Krüger-Barvels 1996), vergleichen zu können, wurden die Ortungslaute der Fledermäuse entsprechend der Einteilung bei Schminke nach zeitlichen Kriterien wie folgt unterschieden:

Vorbeiflüge (VF): kurze Rufsequenzen, die einen Mindestabstand von 90 Sekunden aufweisen.

Suchflüge (SF): kurze Rufsequenzen (wie VF), die sich jedoch innerhalb von 90 Sekunden wiederholen.

Dauersuchflüge (DSF): länger andauernde Ruffolgen, die als Einzelrufe nicht mehr gezählt werden können (gemessen in Sekunden).

Zusätzlich zu diesen Parametern wurden die Zahl der „final buzzes" registriert (erhöhte Frequenz der Ortungsrufe kurz vor der Erbeutung eines Insektes, vgl. z. B. Kalko und Braun 1991). Sie wurden als Beutefangversuche gewertet.

Die Artbestimmung jagender Fledermäuse anhand ihrer Ortungslaute ist im Freiland nur eingeschränkt möglich (Ahlen 1981; Weid und Helversen 1987). Leise rufende Arten wie *Myotis emarginatus* oder *Plecotus* sp. werden mit dem Bat-Detektor kaum gehört. Deshalb wurde versucht, die in den einzelnen Biotopen jagenden Arten zusätzlich über Sichtbeobachtungen bzw. durch Netzfänge (Japannetze) zu bestimmen, auch wenn diese Methoden gleichfalls selektiv sind (Gaisler 1973). Netzfänge erfolgten in 20 Nächten. Sie begannen bei Sonnenuntergang und wurden meist um Mitternacht beendet.

Bei jedem Besuch einer Probestelle wurden weiterhin folgende Daten zum Klima und zum Nahrungsangebot erhoben:

Lufttemperatur: Windstärke: 0 = Windstille, keine Bewegungen an der Vegetation; 1 = Blätter bewegen sich; 2 = Zweige bewegen sich; 3 = Äste bewegen sich; 4 = Bäume schwanken.
Niederschlagsstärke: 0 = trocken; 1 = Sprühregen; 2 = leichter Regen; 3 = starker, anhaltender Regen.
Insektenflug: Dazu wurden mit einer Halogentaschenlampe Wasserfläche und Ufer aufgehellt und die im Lichtstrahl sichtbaren Fluginsekten abgeschätzt (vgl. Taylor und O'Neill 1988): 0 = kein Insektenflug; 1 = vereinzelt Insekten; 2 = regelmäßig Insekten sichtbar; 3 = viele Fluginsekten.

Datenauswertung

Schminke (unpubl.) verwendete als Maß für die Jagdaktivität eine Größe, in die Suchflüge (SF), Dauersuchflüge (DSF) und final buzzes (FB) eingehen und die, bei konstanter Verweildauer an jedem Ort (hier 10 min), einen direkten Vergleich einzelner Probestellen erlaubt. Die Berechnung dieses Jagdaktivitäts-Koeffizienten (JAK) erfolgt nach folgender Formel:

$$\text{JAK} = (\text{Summe der SF} + \text{Summe der DSF}/10) \times (\text{Summe der FB} + 1)$$

Suchflüge und Dauersuchflüge werden dabei zusammengefaßt. Schminke (unpubl.) geht davon aus, daß eine Fledermaus, die in größeren Runden jagt, nach ca. 10 Sekunden wieder dieselbe Stelle passiert. Auf diese Weise bekommt ein Suchflug dieselbe Wertigkeit wie 10 Sekunden Dauersuchflug. Zur Summe der final buzzes wird 1 addiert, da sich sonst eine Jagdaktivität von 0 ergibt, wenn kein final buzz gehört wurde. Aus Gründen der Vergleichbarkeit wurde der Koeffizient hier ebenfalls verwendet, obwohl die Wertung der einzelnen Parameter im JAK etwas subjektiv erscheint.

Da die einzelnen Gewässer unterschiedlich oft (30–35 mal) aufgesucht wurden, werden die JAK-Werte jeweils als arithmetische Mittelwerte aller Besuche angegeben. Die Jagdaktivitäts-Koeffizienten wurden für die Gattungen *Myotis* und *Pipistrellus* getrennt berechnet. Als einzige weitere Gattung konnte *Nyctalus* durch Rufe nachgewiesen werden. Sie wurde aufgrund ihrer Seltenheit gesondert behandelt. Bei der Auswertung wurden folgende Tests verwendet (nach Lamprecht 1992): Mann-Whitney-U-Test, Kruskal-Wallis-H-Test, Spearmans Rangkorrelationskoeffizient (rs). Alle Tests wurden zweiseitig durchgeführt. Als signifikant wurden Ergebnisse ab einer Irrtumswahrscheinlichkeit von $p < 0{,}05$ gewertet.

Ergebnisse

Klimatische Faktoren und Insektendichte

An allen Gewässern beeinflußten die klimatischen Bedingungen deutlich die Jagdaktivität. Jagdflüge fanden erst ab einer Temperatur von 8 °C statt. Bei Windstille und Windstufe 1 war die Jagdaktivität am höchsten (Tab. 1). Bei Windstufe 2 kam es zu einem starken

Tabelle 1. Mittelwerte der Jagdaktivitäts-Koeffizienten von *Myotis* sp. bzw. *Pipistrellus* sp. bei den jeweiligen Wind- bzw. Niederschlagsstärken und Insektendichten (JAK *Myo*: Jagdaktivitäts-Koeffizient von *Myotis* sp., JAK *Pip*: Jagdaktivitäts-Koeffizient von *Pipistrellus* sp. n: Anzahl der Beobachtungen)

Windstärke	JAK-*Myo*	JAK-*Pip*	n	Niederschlag	JAK-*Myo*	JAK-*Pip*	n	Insektendichte	JAK-*Myo*	JAK-*Pip*	n
0	177	55	350	0	163	64	782	0	21	10	297
1	191	71	345	1	94	33	51	1	117	56	349
2	46	14	123	2	59	2	28	2	319	108	186
3	21	25	47	3	0,1	0	10	3	567	210	39
4	0,5	0,2	6								

Einbruch (Rückgang um 75%) der Aktivität, bei Windstufe 4 fanden nur noch einzelne Suchflüge statt. Mit zunehmender Niederschlagsstärke nahm die Jagdaktivität deutlich ab (Tab. 1). Bei starkem Regen (Stufe 3) wurden nur noch einzelne Vorbeiflüge gehört. Für *Myotis* sp. waren die Unterschiede bei verschiedenen Windstufen- und Niederschlagsintensitäten signifikant (H-Test). Mit zunehmender Insektendichte ging auch eine gesteigerte Jagdaktivität einher (Tab. 1). Die Jagdaktivitäts-Koeffizienten bei verschiedenen Insektenhäufigkeiten unterschieden sich signifkant (H-Test). Dieser Zusammenhang beruhte nicht nur auf einer parallelen Entwicklung von Insektendichte und Jagdaktivität im Lauf des Untersuchungszeitraumes. Auch bei kurzfristigen Schwankungen des Nahrungsangebotes an einer Untersuchungsstelle veränderte sich die Jagdaktivität in entspechender Weise.

Die Insektendichte stand ihrerseits mit den klimatischen Faktoren in Zusammenhang. Sie nahm mit der Temperatur zu ($rs = 0{,}4$) und mit ansteigender Windstärke ab ($rs = -0{,}6$). Beide Korrelationen sind signifikant. Bei starkem Regen (Stufe 3) ging die Insektendichte signifikant zurück.

Vergleich von Bächen und Teichen

Die Jagdaktivität von *Myotis* sp. war an Teichen (N = 14 JAK-Mittelwert: 169) um 32% höher als an Bächen (N = 13 JAK-Mittelwert: 128). Dieser signifikante Unterschied (U-Test) wurde vor allem von der höheren Zahl von final buzzes an den Teichen verursacht, die bei der Berechnung des Jagdaktivitäts-Koeffizienten (JAK) relativ hoch gewichtet werden. Insgesamt war allerdings an allen Bächen Flugaktivität zu verzeichnen, während einige Teiche kaum oder gar nicht frequentiert wurden.

Für *Pipistrellus* sp. waren Bäche von geringer Bedeutung (mittlerer Jagdaktivitäts-Koeffizient: 0,5). Auch Bachabschnitte nahe bekannter Kolonien (Entfernung ca. 500 m) wurden kaum bejagt. Dagegen stellten Teiche wichtige Jagdgebiete dar (JAK-Mittelwert: 104).

Jagdaktivität an Teichen

Wald- und Freilandteiche

Myotis sp. bejagte Waldteiche intensiver als Freilandteiche (Tab. 2). Bevorzugt wurden Teilflächen unter überhängenden Zweigen (*Salix* sp., *Quercus robur*). *Pipistrellus* sp. suchte hingegen fast nur an Stillgewässern im Freiland nach Nahrung. Wurde *Pipistrellus* im Wald beobachtet, so jagten die Tiere in einer Höhe von ca. 3–10 m entlang der Vegetationssäume oder in Höhe der Baumgipfel und nicht nahe der Wasseroberfläche. Im Freiland jagte *Pipistrellus* hingegen in einer Höhe zwischen 2 und 5 m, wobei auch Sturzflüge bis auf die Wasseroberfläche erfolgten.

Tabelle 2. Vergleich der Jagdaktivität (JAK) an Wald- und Freilandteichen in Beziehung zu Temperatur, Windstärke und Insektendichte. Angegeben sind jeweils die gewogenen Mittelwerte aller Besuche (n) an den 4 Wald- und den 11 Freilandteichen

	JAK-*Myotis*	JAK-*Pipistrellus*	Temperatur	Wind	Insekten
Waldteiche (n = 128)	336	20	14,8 °C	0,5	1,2
Freilandteiche (n = 355)	154	135	14,1 °C	1,1	0,1

An den 4 Waldteichen war es windstiller und wärmer, und es flogen mehr Insekten als an den 11 Freilandteichen (Tab. 2). Alle Unterschiede (Jagdaktivität, Klima, Insekten) waren signifikant (U-Test).

Da Fledermäuse an einigen Freilandteichen intensiv, an anderen hingegen kaum jagten, wurde dieser Gewässertyp nochmals genauer analysiert und in zwei Gruppen eingeteilt, die sich hinsichtlich der Jagdaktivität signifikant unterschieden (U-Test):
Gruppe 1: Teiche mit geringer Jagdaktivität: JAK < 100 (n = 6)
Gruppe 2: Teiche mit hoher Jagdaktivität: JAK > 100 (n = 5)

Teiche der Gruppe 1 wiesen im Schnitt weniger Ufergehölze, eine geringere Insektendichte, eine niedrigere Lufttemperatur und eine höhere Windstärke auf, als Gewässer der Gruppe 2 (Tab. 3). Abgesehen von der Temperaturdifferenz waren die Unterschiede signifikant (U-Test). Zusätzlich fehlte bei 3 Teichen der Gruppe 1, doch nur bei einem Teich der Gruppe 2 eine „Anbindung“ durch lineare Landschaftselemente an Wälder oder Siedlungen (Quartierstandorte).

Tabelle 3. Freilandteiche mit geringer (Gruppe 1) und hoher Jagdaktivität (Gruppe 2): JAK: mittlere Jagdaktivitäts-Koeffizienten, % UG: Prozent gehölzbestandenes Ufer (Mittelwerte), T: mittlere Temperatur, W: durchschnittliche Windstärke, I: durchschnittliches Insektenangebot; bei JAK, T, W und I sind die gewogenen Mittelwerte aller Begehungen angegeben

	% UG	JAK-*Myotis*	JAK-*Pipistrellus*	T	W	I
Gruppe 1 (n = 6)	25	12	15	13,2	1,3	0,6
Gruppe 2 (n = 5)	90	320	286	14,7	0,7	1,2

Fischbesatz

13 von 15 Teichen waren mit Fischen besetzt. In 5 Fällen erfolgte eine Futterzugabe. Es bestand kein signifikanter Unterschied hinsichtlich der Jagdaktivität zwischen den intensiv bewirtschafteten Teichen mit Zufütterung und den anderen Gewässern. Allerdings wurden sowohl bei *Myotis* sp. als auch bei *Pipistrellus* sp. die höchsten JAK-Tageswerte (über 400) an den Teichen mit Futterzugabe erreicht.

Jagdaktvität an Bächen

Da *Pipistrellus* sp. an Bächen kaum jagt, wurden in der folgenden Auswertung die addierten Jagdaktivtäts-Koeffizienten von *Myotis* sp. und *Pipistrellus* sp. verwendet.

Vergleich von Wald- und Freilandbächen:

Die Jagdaktivität war an den 8 Probestellen im Freiland deutlch höher als an den 4 Orten im Wald (Tab. 4), doch ist der Unterschied nicht signifikant (U-Test). Dies ist auf die große Variabilität der Aktivität an den Freilandbächen zurückzuführen. Die durchschnittlichen Werte für die Windstärke waren an beiden Bachgruppen etwa gleich (Tab. 4), doch wiesen Freilandbäche ein signifikant höheres Insektenangebot auf (U-Test).

Im Gegensatz zu den Freilandteichen ließen sich bei den Freilandbächen keine Gruppen mit deutlich unterschiedlicher Jagdaktivität der Fledermäuse bilden. Insgesamt war die Jagdaktivität an den Freilandbächen mit der Insektendichte signifikant positiv korreliert (rs = 0,7) und ging mit zunehmender Windstärke (allerdings nicht signifikant) zurück (Abb. 1). An den 5 Probestellen mit dichtem Ufergehölz war sie höher als an den 3 Bachabschnitten mit spärlicher oder fehlender Gehölzvegetation (JAK-Mlittelwerte: 111 und 67). Doch auch dieser Unterschied war nicht signifikant.

Tabelle 4. Vergleich der Jagdaktivität (JAK) an Wald- und Freilandbächen in Beziehung zu Temperatur, Windstärke und Insektendichte. Angegeben sind jeweils die gewogenen Mittelwerte aller Besuche

	JAK	Temperatur	Wind	Insekten
Waldbäche (n = 4)	56	14,9 °C	0,9	0,7
Freilandbäche (n = 8)	94	14,6 °C	0,8	1,0

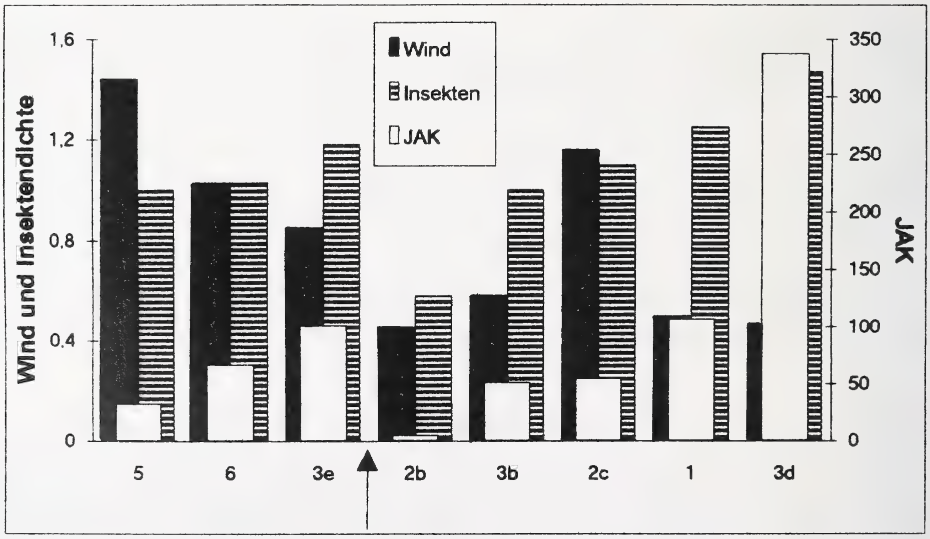


Abb. 1. Durchschnittswerte der Windstärke, der Insektendichte und der Jagdaktivität (JAK) an den Bächen im Freiland. Links des Pfeils: Freilandbäche ohne Gehölzbewuchs; Rechts des Pfeils: Freilandbäche mit Ufergehölzen. Ziffern: Bezeichnung der Bäche, Buchstaben: Bezeichnung verschiedener Untersuchungsstellen an einem Bach.

Dort, wo viele Äste in den Luftraum über der Wasseroberfläche ragten, wurden nur wenig jagende Fledermäuse beobachtet. Die höchste Aktivität wurde an Stellen registriert, die zwar mit Bäumen bestanden waren, jedoch bis in 3 m Höhe über der Wasseroberfläche einen offenen Luftraum aufwiesen (JAK: 107 und 337). Hier gab es auch die meisten Insekten. Die geringste Jagdaktivität an Uferbereichen mit Gehölzen wurde an zwei Stellen festgestellt, an denen Hindernisse im Bach einen hohen Geräuschpegel verursachten und die Gewässeroberfläche sehr unruhig war (JAK: 51 und 7). An Abschnitten mit spärlichem Uferbewuchs wurden Fledermäuse vor allem im Bereich der wenigen Bäume und Sträucher registriert.

Ein Einfluß der Fließgeschwindigkeit von Bächen auf die Jagdaktivität konnte nicht nachgewiesen werden.

Bei der Untersuchung der Gewässergüte an den Bächen wurden die Güteklassen I–II (4×), II (5×) und II–III (3×) festgestellt. Die Bachabschnitte mit der Güteklasse I–II wiesen die höchste Jagdaktivität (mittlerer JAK: 163) und die meisten Insekten auf (Mittelwert: 1,1). Betrachtet man die Bäche der Güteklassen II (mittlerer JAK: 37, mittlere Insektendichte: 0,8) und II–III (mittlerer JAK: 58, mittlere Insektendichte: 1,0), so zeichnet sich kein klarer Zusammenhang zwischen Gewässergüte und Insektenangebot bzw. Jagdaktivität ab.

Netzfänge

Insgesamt wurden 31 Tiere an den untersuchten Gewässern gefangen. Die häufigsten Arten waren *Myotis mystacinus* (n = 10) und *Myotis daubentoni* (n = 10). Weiterhin gingen 4 *Myotis emarginatus*, 4 *Myotis myotis*, 2 *Pipistrellus pipistrellus* und 1 *Myotis nattereri* ins Netz. Eindeutige Biotoppräferenzen einzelner Arten ließen sich aus Materialmangel nicht belegen.

Aktivität von *Nyctalus* sp. im Untersuchungsgebiet

Jagdaktivität von Abendseglern (*Nyctalus noctula*) wurde nur im Mai sowie im September und Oktober registriert. Die Tiere jagten bevorzugt in der ersten Stunde nach Sonnenuntergang in einer Höhe von ca. 20 m im freien Flugraum über großen Teichen, teilweise aber auch über den Baumgipfeln an Waldteichen. Im September waren sie vereinzelt auch über Bächen in einer Höhe von ca. 10 m zu beobachten.

Diskussion

Bat-Detektor und Netzfänge erfassen die Fledermausaktivität bzw. das Artenspektrum selektiv. Deshalb kann man aus der vorliegenden Untersuchung nicht schließen, daß Gewässer, an denen wenig Jagdaktvität nachgewiesen wurde, als Nahrungshabitat keine Rolle spielen, bzw. daß nur die im Netz gefangenen Arten an einer Probestelle vorkommen. Umgekehrt kann man allerdings sagen, daß Gewässertypen, an denen eine hohe Jagdaktivität verzeichnet wurde, in jedem Fall für Fledermäuse von großer Bedeutung sind.

Insektenreichtum und Windschutz erwiesen sich als entscheidende Voraussetzungen für ein optimales Jagdhabitat. Dieser Zusammenhang wurde auch von anderen Autoren festgestellt (Kunz 1973; Racey und Swift 1985; Taylor und O'Neill 1988; Walsh und Mayle 1991). Windschutz begünstigt das Vorkommen von Insekten und deren Flugaktivität (Grimmberger 1979; Nyholm 1965). Zudem vermutet Grimmberger (1979) bei kleineren Fledermausarten eine Beeinträchtigung der Flugmechanik durch starken Wind.

Vergleicht man Fließ- und Stillgewässer, so fällt auch hier der Zusammenhang zwischen Nahrungsangebot und jagenden Fledermäusen auf. Im Wald wurden an Teichen

durchschnittlich höhere Insektendichten und Jagdaktivitätskoeffizienten festgestellt als an Bächen. Der gleiche Unterschied bestand auch zwischen Freilandteichen mit Ufergehölzen und gehölzbestandenen Bachabschnitten. An Freilandbächen ohne bzw. mit spärlicher bachbegleitender Gehölzvegetation wurden allerdings höhere Insektendichten und Jagdaktivitäten festgestellt als an Freilandteichen ohne Gehölzbewuchs. Möglicherweise spielen unbewachsene Bachabschnitte im Gegensatz zu den Teichen auch als Flugweg eine gewisse Rolle. Insgesamt wurde an den Stillgewässern intensiver gejagt als an den Fließgewässern. Dies wurde auch von Fenton (1970) festgestellt. Doch muß dies nicht überall gelten, da das für die Jagdaktivität entscheidende Nahrungsangebot an Teichen nicht generell höher sein muß als an Bächen.

Freilandteiche, an denen intensiv gejagt wurde, lagen nahe an linearen Landschaftselementen wie Hecken, die von einigen Fledermausarten als Flugwege genutzt werden (Limpens und Kapteyn 1991; Rieger et al. 1990; Rieger und Alder 1993). Doch waren die betreffenden Teiche auch gehölzbestanden und insektenreich, so daß nicht klar wurde, wie bedeutend in diesen Fällen die linearen Landschaftselemente sind.

An Bächen schienen Turbulenzen und Rauschen die Jagd zu erschweren. So flogen an einer Probestelle kaum noch Fledermäuse, als der Bach in den Tagen nach einem Unwetter mehr Wasser führte und laut über eine Steinsohle rauschte. Schminke (unpubl.) nimmt an, daß Rauschen bei 10–40 kHz die Echoortung stören könnte. Weiterhin wirkten sich Äste und Zweige, die in den Flugraum ragten, bei schmaleren, beidseitig bewachsenen Bächen negativ auf die Fledermausaktivität aus.

Der Nährstoffreichtum der untersuchten Bäche hatte keinen erkennbaren Einfluß auf die Jagdaktivität. Helversen et al. (1987) merken an, daß die Eutrophierung von Gewässern eine Steigerung der Insekten-Biomasse bedingt. Bei den untersuchten Bächen nahm das Insektenangebot mit der organischen Belastung der Bäche nicht zu. Möglicherweise verdeckte der Einfluß des Umlandes (Insektenangebot durch Ufergehölze) unterschiedliche Häufigkeiten fliegender Wasserinsekten.

Vergleicht man die untersuchten Gewässer mit anderen Biotopen im selben Gebiet, an denen die Jagdaktivität mit der gleichen Methode erhoben wurde, so ergaben sich an Gewässern erheblich höhere Jagdaktivitäts-Koeffizienten (Maximalwerte 658 bei Bächen und 573 bei Teichen) als in Wäldern (maximaler JAK: 63; Zahn und Krüger-Barvels 1996) oder in Feldgehölzen, Obstwiesen, Gärten und an Straßen (maximale JAK < 100; Schminke, unpubl.). Zwar mag sich die Nachweisbarkeit der Fledermäuse in den untersuchten Habitaten unterscheiden, so daß diese Werte nicht direkt vergleichbar sind, doch wird deutlich, daß Gewässer wohl zu den besonders intensiv bejagten Biotoptypen im Untersuchungsgebiet zählen.

Bemerkungen zu einzelnen Arten

Bei den beobachteten *Pipistrellus* sp. handelte es sich wohl um die im Gebiet nachgewiesene Zwergfledermaus (*Pipistrellus pipistrellus*). Sie bevorzugte gehölzbestandene Stillgewässer im Freiland und jagte besonders entlang der Gehölzvegetation (meist auf der Lee-Seite) in Gewässernähe. Teiche ohne Ufervegetation waren als Jagdbiotope gänzlich unattraktiv. Im Wald wurden Zwergfledermäuse nur vereinzelt über Gewässern auf Lichtungen gehört, die zudem am Rande der Waldgebiete in Ortsnähe (< 1 km Entfernung) lagen und durch Waldwege mit dem Freiland verbunden waren, was den Anflug begünstigen könnte. Über dicht mit Gehölzen bestandenen Bächen wurde die Art nie beobachtet, doch flog sie in solchen Fällen manchmal am Außenrand der bachbegleitenden Gehölze entlang. Auch jagten Zwergfledermäuse regelmäßig an einem teichartig verbreiterten Bachabschnitt am Waldrand. Ähnliche Habitatpräferenzen wurden von Sachteleben (unpubl.) sowie Racey und Swift (1985) festgestellt.

Die Arten der Gattung *Myotis* waren anhand der Rufe nicht eindeutig zu unterscheiden. Aufgrund von Sichtbeobachtungen konnte jedoch oft auf die Anwesenheit von Wasserfledermäusen (*Myotis daubentoni*) geschlossen werden: Diese Art jagt ausgiebiger und dichter als andere über dem Wasser (0,05–0,3 m) und fängt Beutetiere zum Teil direkt von der Oberfläche (Kalko und Braun 1991; Nyholm 1965; Rieger et al. 1992; Schober und Grimmberger 1987; Taake 1992). Bevorzugt wurden von den Wasserfledermäusen Gewässer außerhalb des Waldes. Bei Wind jagten sie an wenig geschützten Teichen bevorzugt nahe der Vegetation, an Gewässern mit gutem Windschutz hingegen mehr über der freien Wasserfläche. Der Fang von drei Wimperfledermäusen (*Myotis emarginatus*) an einem Bach zur Zeit des Ausflugs einer nahegelegenen Kolonie deutet auf die Nutzung von Fließgewässern als Flugrouten hin. Dies vermuten auch Krull et al. (1991).

Die Kleine Bartfledermaus (*Myotis mystacinus*), wurde durch Netzfänge und gleichzeitige Beobachtungen an allen Gewässertypen mit Ufergehölzen jagend nachgewiesen. Bäche dienen Bartfledermäusen wohl nicht nur als Flugrouten sondern werden noch drei bis fünf Stunden nach Sonnenuntergang intensiv bejagt. Der Große Abendsegler (*Nyctalus noctula*) wurde nur im Frühjahr und Herbst angetroffen. Zu diesen Zeiten findet in Bayern ein starker Durch- bzw. Zuzug von Abendseglern statt (Weid, mdl.). Die Art wurde nur an größeren Gewässern mit freiem Luftraum beobachtet. Zugewachsene Kleingewässer und Bäche dürften für diese Art als Jagdgebiet ungeeignet sein.

Danksagungen

Wir danken Prof. Dr. G. Neuweiler, H. Geiger und M. Meinl für die kritische Durchsicht des Manuskripts. Bei den Freilandarbeiten halfen G. Friedel, M. Seif, M. Thalmeier, V. Rief, K. Enz, A. Unsin, M. Zehner, U. Rindle und A. Tiplt.

Zusammenfassung

Von Mai bis Oktober 1993 wurde die Jagdaktivität von Fledermäusen an Teichen und Bächen (27 Probestellen) mit Bat-Detektoren und durch Netzfänge ermittelt. Für das Untersuchungsgebiet im Südosten Oberbayerns sind folgende Fledermausarten belegt: *Nyctalus noctula, Pipistrellus pipistrellus, Myotis myotis, Myotis emarginatus, Myotis mystacinus, Myotis daubentoni, Myotis nattereri, Myotis brandti, Myotis bechsteini, Eptesicus serotinus, Plecotus auritus, Barbastella barbastellus, Rhinolophus hipposideros.* Die ersten 7 Arten wurden im Lauf der Untersuchung an den Gewässern nachgewiesen. An gehölzbestandenen Gewässern wurde eine höhere Jagdaktivität registriert als an unbewachsenen Bächen und Teichen. Isoliert im Freiland liegende Teiche ohne Ufervegetation wurden völlig gemieden und auch an Bächen wurden nur wenig Fledermäuse gehört, wenn Bäume und Sträucher fehlten. Engten Ufergehölze den Flugraum stark ein, wurden ebenfalls nur wenige Tiere registriert. Im Wald wurde an Teichen mehr gejagt als an Bächen. Der gleiche Unterschied bestand zwischen Freilandteichen mit Ufergehölzen und gehölzbestandenen Bachabschnitten.

Als entscheidende Faktoren für die Nutzung einer Untersuchungsstelle durch Fledermäuse erwiesen sich Windschutz und Insektenangebot. Hoher Fischbesatz wirkte sich nicht negativ auf die Jagdaktivität aus. Ein Einfluß des Eutrophierungsgrades der Fließgewässer konnte nicht festgestellt werden.

Literaturverzeichnis

Ahlen, J. (1981): Identification of Scandinavian bats by their sounds. Uppsala: Swedish Univ. Agricult. Sci. Report 6.

Audet, D. (1990): Foraging behavior and habitat use by a gleaning bat, *Myotis myotis* (Chiroptera: Vespertilionidae). J. Mammalogy **71**, 420–427.

Baur, W. H. (1980): Gewässergüte bestimmen und beurteilen. Hamburg, Berlin: Paul Parey.

Degn, H. J. (1983): Field activity of a colony of serotine bats (*Eptesicus serotinus*). Nyctalus (N. F.) **1**, 521–530.

Fenton, M. B. (1970): A technique for monitoring bat activity with results obtained from different environments in southern Ontario. Can. J. Zool. **48**, 847–851.

Gaisler, J. (1973): Netting as a possible approach to study bat activity. Perod. biol. **75**, 129–143.

Grimmberger, E. (1979): Untersuchungen über den Einfluß klimatischer Faktoren auf das Verhalten der Zwergfledermaus, *Pipistrellus pipstrellus* (Schreber 1774), im Winterquartier und während der sogenannten Invasionen. Nyctalus **2**, 145-157.

Helmer, W.; Limpens, H. J. G. A. (1991): Echos in der Landschaft – Über Fledermäuse und ökologische Infrastruktur. Dendrocops **18**, 3–8.

Helversen, O. von; Esche, M.; Kretschmar, F.; Boschert, M. (1987): Die Fledermäuse Südbadens. Mitt. bad. Landesver. Naturkunde u. Naturschutz, N. F. **14**, 409–475.

Kalko, E.; Braun, M. (1991): Foraging areas as an important factor in bat conservation: estimated capture attempts and success rate of *Myotis daubentoni* (Kuhl, 1819). Myotis **29**, 55–60.

Klawitter, J. (1988): Einrichtung von Fledermauswinterquartieren. Schriftenreihe Bayer. Landesamt für Umweltschutz **81**, 71–58.

Kronwitter, F. (1988): Population structure, habitat use and activity pattems of the noctule bat, *Nyctalus noctula*, revealed by radio-tracking. Myotis **26**, 23–85.

Krull, D.; Schumm, A.; Metzner, W.; Neuweiler, G. (1991): Foraging areas and foraging behavior in the notch-eared bat, *Myotis emarginatus* (Vespertilionidae). Behav. Ecol. Sociobiol. **28**, 247–253.

Kunz, T. H. (1973): Resource utilisation: Temporal and spatial components of bat activity in central Iowa. J. Mammalogy **54**, 14–32.

Lamprecht, J. (1992): Biologische Forschung: Von der Planung bis zur Publikation. Berlin, Hamburg: Paul Parey.

Limpens, H. J. A. G.; Kapteyn, K. (1991): Bats, their behaviour and linear landscape elements. Myotis **29**, 39–48.

Maywald, A.; Pott, B. (1988): Fledermäuse – Leben. Gefährdung, Schutz. Ravensburg: Otto Maier.

Nagel, A.; Richarz, K. (1994): Rückgang der Fledermäuse und ihr Schutz. In: Die Fledermäuse Hessens, Hrsg. von der Arbeitsgemeinschaft für Fledermausschutz in Hessen. Remshalden: Verlag Manfred Hennecke. Pp. 141–158.

Nyholm, E. S. (1965): Zur Ökologie von *Myotis mystacinus* Leisler und *Myotis daubentoni* Leisler (Chiroptera). Ann. Zool. Fenn. **2**, 77–123.

Racey, P. A.; Swift, S. M. (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. J. Anim. Ecol. **54**, 205–215.

Rachwald, A. (1992): Habitat preference and activity of the noctule bat *Nyctalus noctula* in the Bialowieza Primeval Forest, Acta Theriol. **37**, 413–422.

Richarz, K. (1986): Bedrohung und Schutz der Gebäudefledermäuse. Schriftenreihe Bayer. Landesamt Umweltschutz **73**, 15–35.

Richarz, K. (1994): Situation und Perspektiven des Fledermausschutzes in Hessen. In: Die Fledermäuse Hessens, Hrsg. von der Arbeitsgemeinschaft für Fledermausschutz in Hessen. Remshalden: Verlag Manfred Hennecke. Pp. 11–32.

Richarz, K.; Krull, D.; Schumm, A. (1989): Quartieransprüche und Quartierverhalten einer Mitteleuropäischen Wochenstubenkolonie von *Myotis emarginatus* im Rosenheimer Becken, Oberbayern, mit Hinweisen zu den derzeit bekannten Wochenstubenquartieren dieser Art in der BRD. Myotis **27**, 111–130.

Richarz, K.; Limbrunner, A. (1992): Fledermäuse: fliegende Kobolde der Nacht. Stuttgart: Franckh-Kosmos.

Rieger, I.; Walzthöny, D.; Alder, H. (1990): Wasserfledermäuse, *Myotis daubentoni*, benutzen Flugstraßen. Mitt. natf. Ges. Schaffhausen **35**, 37–68.

Rieger, I. ; Alder, H.; Walzthöny, D. (1992): Wasserfledermäuse, *Myotis daubentoni*, im Jagdhabitat über dem Rhein. Mitt. natf. Ges. Schaffhausen **37**, 1–34.

Rieger, I.; Alder, H. (1993): Weitere Beobachtungen von Wasserfledermäusen, *Myotis daubentoni*, auf Flugstraßen. Mitt. natf. Ges. Schaffhausen **38**, 1–34.

Schober, W.; Grimmberger, E. (1987): Die Fledermäuses Europas: kennen – bestimmen – schützen. Stuttgart: Franckh-Kosmos.

Schumm, A.; Krull, D.; Neuweiler, G. (1991): Echolocation in the notch-eared bat, *Myotis emarginatus*. Behav. Ecol. Sociobiol. **28**, 255–261.

SWIFT, S. M.; RACEY, P. A.; AVERY, M. I. (1985): Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. II. Diet. J. Anim. Ecol. **54**, 217–225.

TAAKE, K.-H. (1984): Strukturelle Unterschiede zwischen den Sommerhabitaten von Kleiner und Großer Bartfledermaus (*Myotis mystacinus* und *Myotis brandti*) in Westfalen. Nyctalus **2**, 16–32.

TAAKE, K.-H. (1992): Strategien der Ressourcennutzung an Waldgewässern jagender Fledermäuse (Chiroptera: Vespertilionidae). Myotis **30**, 7–73.

TAYLOR, R. J.; O'NEILL, M. G. (1988): Summer activity patterns of insectivorous bats and their prey in Tasmania. Aust. Wildl. Res. **15**, 335–339.

WALSH, A. L.; MAYLE, A. B. (1991): Bat activity in different habitats in a mixed lowland woodland. Myotis **29**, 97–104.

WEID, R.; HELVERSEN, O. VON (1987): Ortungsrufe europäischer Fledermäuse beim Jagdflug im Freiland. Myotis **25**, 5–27.

ZAHN, A.; KRÜGER-BARVELS, K. (1996): Wälder als Jagdhabitate von Fledermäusen. Z. Ökologie u. Naturschutz **5**, 77–84.

Anschr. der Verf.: Dr. ANDREAS ZAHN und SANDRA MAIER, Zoologisches Institut, Universität München, Postfach 20 21 36, D-80021 München

Z. Säugetierkunde **62** (1997) 12–22

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Spatial organization and habitat utilization of badgers *Meles meles*: effects of food patch dispersion in the boreal forest of central Norway

By H. Brøseth, B. Knutsen, and K. Bevanger

Norwegian Institute for Nature Research, Trondheim, Norway

Receipt of Ms. 08. 12. 1995
Acceptance of Ms. 17. 09. 1996

Abstract

Habitat utilization, home range size and territory size in relation to food availability for badgers (*Meles meles* L.) were studied for eight months in coniferous forest influenced by agricultural activity in central Norway. The diet in both spring and autumn was dominated by earthworms; berries formed only an insignificant part of it in autumn. Earthworms in soil samples were unevenly distributed among different biotopes, with the highest earthworm biomass found in deciduous forest. Earthworm biomass was higher under cowpats on pasture, which increased the predictability of potential badger food. There was no difference in the composition of the home ranges between spring and autumn, but different biotopes within them were utilized. Deciduous forest was much used in both seasons, and the use of pastures increased in autumn. The dispersion of patches of deciduous forest within the group territories accounted for much of the observed variation in territory size.

Introduction

The dispersion and abundance of resources affects spatial and social organization in many birds and mammals (e. g. Davies 1991). The resource dispersion hypothesis (RDH) predicts that spatial organization will be determined by the dispersion of resource patches and that group size will be determined by the richness of these patches when animals occupy the smallest economically defendable area (Macdonald 1983 a; Kruuk and Macdonald 1985).

The European badger (*Meles meles* L.) has received much attention in connection with theories on the evolution of group living in carnivores, but we do not fully understand the advantages that influence this solitary forager to select group living in many populations. Attempts to explain the spatial and social organization of badgers have centred around food dispersion (e. g. Kruuk and Parish 1982; Macdonald 1983 a; Kruuk and Macdonald 1985; Woodroffe and Macdonald 1993). Spatial organization has been classified as territorial, with territories of a minimum size (Kruuk and Macdonald 1985), and the RDH permits one to predict that for a given food patch richness, territories will be larger where patches are more dispersed (Macdonald 1983 a).

Within the wide geographical distribution area of the badger in the Palaearctic (Neal 1986) there is a great variation in spatial and social organization among different badger populations, from groups to a solitary lifestyle (Woodroffe and Macdonald 1993). Many populations form stable social groups with 3–29 individuals (Cheeseman et al. 1987; Silva et al. 1994) of mixed age and sex where the members share a territory and occupy communal setts, but forage alone (Kruuk 1978). These groups are formed mainly by retention

of individuals in their natal territory (Silva et al. 1994). Within the group territory, individual badgers can have different ranges (Kruuk 1989), and home ranges vary in size from 14 ha (Gloucestershire, England: Cheeseman et al. 1981) to 983 ha (Doñana, Spain: Rodrigues et al. 1996).

With regard to food, badgers are characterised as opportunists (reviewed in Roper 1994). Studies have shown that different food can dominate in the diet of badgers, e. g. cereals (Shepherdson et al. 1990), fruits and insects (Pigozzi 1991), fruits (Rodríguez and Delibes 1992) and rabbits (Martín et al. 1995). In common with many other studies on the diet of badgers in northern Europe (e. g. Kruuk and Parish 1981; Lüps et al. 1987; Neal 1988), investigations in Scandinavia have shown that earthworms are the most important prey (Skoog 1970; Lindström 1989). But, food consumption and the utilization of different types of food can be expected to change during the year as they become available (Kruuk and Parish 1981; Pigozzi 1991). Earthworms are rich in protein, essential amino acids, and fat (Macdonald 1983 b). They are likely to be particularly important in spring and early summer when badgers need to replenish resources used during their winter sleep and reproducing females have their lactation period. Berries, rich in carbohydrate, can be important to build up fat reserves when they become available during the autumn (Lindström 1989).

In this study, we analyse the diet, food availability, habitat utilization, home range size, and territory size of badgers in part of the boreal forest of central Norway, one of the northernmost reproducing badger populations in Scandinavia (Bevanger and Lindström 1995), to evaluate their spatial organization.

Material and methods

Study area

The study was carried out in the municipality of Malvik (63° 18′–63° 27′ N, 10° 35′–10° 57′ E), in the county of Sør-Trøndelag, in 1993. The area is in the middle boreal region and comprises 60 km^2 of coniferous forest affected by agricultural activity, restricted by a river in the north, a lake in the south and hills of high altitude in the east and west (Fig. 1). Heifers and sheep roam freely beyond the fenced-in

Fig. 1. The study area (60 km^2) at Malvik, Sør-Trøndelag county, Norway. Black areas: deciduous forest and agricultural land, grey areas: coniferous forest and fen, white areas: water

farmland from the beginning of June to mid-September. The area is chiefly situated 200–500 m above sea level, but extends above the climatic tree line near its eastern edge; large parts are hilly with rocky slopes. The mean annual temperature is 1.5 °C (January–5.8 °C and July 9.8 °C), the mean annual precipitation is 1260 mm (min. May and max. September), and there are on average 163 days with snow cover (the depth peaking in February–March).

Maps (1 : 5 000) from the Norwegian Mapping Authority and field surveys were used to construct a habitat map over the study area, based on vegetation communities and soil fertility (Tab. 1) (Fremstad and Elven 1987). We vector-digitized the habitat map as a thematic polygon map (Burrough 1986), using a geographical information system (GIS), where polygons divided the habitat into biologically meaningful subunits (biotopes) suitable for analysis in the context of patch theory (Haslett 1990). The software used for creation of the habitat map was PC ArcInfo 3.4 d+ (ESRI 1990). Calculation of total area, mean polygon size and number of polygons for different biotopes were done by importing ArcInfo PAT-files into the software of SPSS for windows, release 6.0 (SPSS Inc. 1993).

Table 1. Biotopes classified in the area studied at Malvik, in the boreal forest of central Norway

Biotope	% of area	Characteristica
Poor coniferous forest	62.2	Coniferous forest on poor soil and rocks. Mainly spruce (*Picea abies*) and some pine (*Pinus sylvestris*). *Vaccinium* spp. common in the field layer.
Rich coniferous forest	17.3	Coniferous forest (spruce) on rich soil. Field layer with some low and tall herbs. >50% of area covered by conifers.
Deciduous forest	1.3	Deciduous and mixed deciduous forest on rich soil. Mainly white birch (*Betula pubescens*) with some aspen (*Populus tremula*), rowan (*Sorbus aucuparia*) and alder (*Alnus incana*). <50% of area covered by conifers. Field layer rich in low and tall herbs.
Fen	10.1	Moist area rich in mosses. Poorly developed tree and shrub layer.
Arable land	3.6	Grassland harvested twice a year. Renewed every 3–5 years by ploughing. Monoculture.
Pasture	1.0	Former arable grassland now harvested by cows (*Bos taurus*) and sheep (*Ovis aries*) from late-June to late-September.
Water	4.5	Small lakes and ponds

Diet identification

Badger faeces were collected from latrines near setts (n = 18) in two periods. Spring samples (n = 35) were taken until mid-July, before the expected diet shift to berries occurs (Skoog 1970). Bilberries (*Vaccínium myrtíllus* L.) were available to the badgers from July 20, cowberries (*V. vitis-idaéa* L.) somewhat later. In mid-July, every known latrine was visited and defecations were removed to avoid confusion between seasons. Autumn samples (n = 30) were taken until mid-October. Only fresh faeces were collected, and an attempt was made to take each sample from only one defecation. Prior to detailed laboratory analysis, they were stored in plastic bags at –18 °C as soon as possible after sampling, to stop the decomposition of earthworm gizzard rings.

Faecal analysis was mainly carried out according to the procedure developed by Kruuk and Parish (1981). Each faecal sample was washed through a mesh sieve (1.25 mm) using 500 ml of water, and three samples (1.5 ml) from each were examined under a 40× binocular microscope for the presence of

earthworm chaetae. The food remains retained in the sieve after additional washing were put into a white tray with water, identified and counted. The line of best fit between the chaetae score (x) and the number of gizzard rings (y) in samples where the latter had not started to decompose was $y = 4.05\,x + 4.00$ ($r = 0.73$, $P < 0.001$, $n = 30$). This line was used to estimate the number of earthworms in samples where counting gizzard rings was impossible or uncertain. The number of gizzard rings give the absolute number of earthworms eaten. To obtain the best weight estimate of earthworms eaten by badgers in the study area, we estimated a mean earthworm weight from earthworm remains found in the stomachs of two dead badgers, victims of road accidents, found less than 3 km from the study area (2.54 g, n = 75).

To show the significance of different food items in the total diet we used frequency of occurrence and weight percentage of consumed fresh biomass, because these two measurements together are thought to give the best estimation of overall diet (Korschgen 1980). To reveal differences in diet between seasons we used the G-test to test for differences in the frequency of occurrence and the Mann Whitney U-test corrected for ties for the biomass consumed.

Earthworm availability

Earthworm availability was estimated by hand sorting (Edwards and Lofty 1977) in randomly selected polygons, six in each biotope, from the digitized map. In each polygon, a position was randomly selected and a rectangle (10×20 m) trending north-south was marked out. Using an iron frame, sample quadrats (20×20×15 cm) were removed for hand sorting at every 10 m, i. e. six samples per polygon. These soil samples were searched by hand in a white expanded polyester box, and all potential badger food was retained. The biomass in the soil samples was determined in the laboratory, and the mean fresh weight (g/m^2) was calculated for every biotope.

To find out whether faeces from domestic animals increased the biomass and the chance of earthworms being present, 18 soil samples that had a cowpat within the iron frame were taken from pasture land. The method was otherwise like that used for hand sorted, random soil samples. We used the Kruskall Wallis test to test for overall differences between biotopes and the Mann Whitney U-test corrected for ties to locate differences. Differences between samples taken under cowpats on pasture and random samples in the same biotope were tested by the Mann Whitney U-test corrected for ties.

Radio tracking

Between March and August 1993, 11 badgers (5 males and 6 females) were trapped at setts, in cage traps or leg-hold traps. The badgers were immobilized by an intramuscular injection of 2.5 ml of ketamine hydrochloride (cf. Cheeseman and Mallinson 1980) and taken to a veterinary surgeon who implanted a transmitter (Telonics: IMP/400/L, 142 MHz) in the abdominal cavity as described by Fowler and Racey (1988). The animals were sexed, weighed, marked with an individual number tattooed on the upper inside of the left hind leg, and a tooth (I^{3V}) was taken for age determination (Ahnlund 1976). Following the surgery, the badgers were given an intramuscular injection of an antibiotic (600 mg benzyl penicillin procain.) and returned to the sett where they were released.

The badgers were located by triangulation on irregular occasions from a car and on foot, using a hand-held, Yagi-type antenna connected to a VHF receiver (Televilt) and a compass (Silva Ranger: Type 15), or by direct observations (10.2%). Bearings were taken from at least two points, the time interval between them being less than five min. and the angle between them being as close to 90° as possible. Animals were located on average 2 times (range 1–5) during their activity period at night for on average 37 nights (range 9–58). Discontinuous locations were preferred because of their applicability in range and habitat utilization analysis (Harris et al. 1990).

Radio-tracking data were collected during two seasons: spring, mid-April to the beginning of July (8 animals), and autumn, the beginning of August to the beginning of October (9 animals). The division into two tracking periods was made because of the expected interseasonal shift in diet, with a consequent change in behaviour. On average, 50 fixes (range 21–65) were made on each animal each season. We calculated individual 95% minimum convex polygons as home range estimators separately for spring and autumn using Ranges IV (Kenward 1990). Territories were estimated by calculating 95% minimum convex polygons from fixes of animals in the same social group (more than 80% overlap in home range and at least three common setts, or for one animal: less than 20% overlap and no common setts). We used telemetry fixes to estimate territories because no boarder markings with latrines were

found, as known from high density populations (cf. Kruuk 1989). The home range- and territory areas were copied as an ASCII text file from Ranges IV to ArcInfo where biotope composition and food patch dispersion could be calculated from the habitat map.

Habitat utilization was compared with availability, excluding water, using compositional analysis to reveal any habitat selectivity (Aebischer et al. 1993a). Home ranges were compared with the study area, and fixes with home ranges. The proportion of fixes in different biotopes was found by creating a point coverage from an ASCII text file with the localizations and overlaying this with the digitized habitat map in ArcInfo. Overall deviation from random utilization was tested with χ^2 as the test statistic, the t-test being used to find where utilization deviated from random, and a ranking in the order of use was created (Aebischer et al. 1993a). A MANOVA-test was used to test for differences in habitat use between seasons (Aebischer et al. 1993b).

To evaluate spatial organization as predicted by the RDH, we analysed territory size in relation to food patch dispersion. A patch was defined as an area at least 20 m from the nearest area of same biotope, and over 0.05 ha in size. These seem to be distinguishable by badgers when foraging (Mellgren and Roper 1986). To measure food patch dispersion, we calculated the overall mean distance from the perimeter of each earthworm-rich patch (deciduous forest) to the perimeter of all other patches of deciduous forest within the territory, using ArcView (ESRI 1992). Regression analysis was used to test how patch dispersion affected the variation in size of the territories. With six badgers followed for both seasons, spring data were randomly selected from three of the animals and autumn data from the other three to use for habitat utilization analysis, together with data from all the badgers followed through one season. This was done to avoid dependence in the data between seasons. When spring and autumn data were analysed separately, every animal was used.

Results

The diet in the study area was dominated by earthworms both in spring (75.7%) and autumn (53.9%) (Tab. 2). There was no difference in the frequency of earthworms in the diet between seasons ($G = 1.04$, $P = 0.31$), but they constituted more of the fresh biomass consumed in spring than in autumn ($z = 3.44$, $P < 0.001$). There was no difference in the berries in the diet between seasons, neither for frequency ($G = 2.95$, $P = 0.09$), nor biomass ($z = 1.82$, $P = 0.07$). Frogs were the only food item showing any sign of seasonal diet shift; they were both taken more often in the autumn ($G = 19.93$, $P < 0.001$) and constituted a larger amount of the autumn diet ($z = 3.98$, $P < 0.001$).

Table 2. Diet of badgers in a boreal forest area in central Norway, expressed as frequency of occurrence (Freq) and percent of consumed fresh biomass in the total diet (% Bio)

Food item	Spring (n = 35)		Autumn (n = 30)	
	Freq	% Bio	Freq	% Bio
Earthworms	1.00	75.7	0.97	53.9
Amphibians (*Rana temporaria*)	0.20	4.5	0.60	25.0
Small rodents	0.29	7.7	0.20	5.7
Birds	0.23	3.4	0.17	3.0
Beetles	0.77	2.4	0.70	1.4
Other insects	0.66	1.5	0.83	3.7
Gastropoda	0.23	0.3	0.20	0.3
Berries	0.06	0.1	0.20	3.6
Carrion and domestic waste	0.20	4.3	0.13	3.2
Other or unidentified	0.14	0.1	0.03	0.2

There were significant differences between biotopes in both total biomass potential badger food ($H = 120.4$, $df = 5$, $P < 0.001$) and earthworm biomass ($H = 124.8$, $df = 5$, $P < 0.001$), based on the soil samples (Tab. 3). Deciduous forest contained a greater earthworm biomass than all the other biotopes (z's all >1.96, P's all <0.05). Samples taken in pasture, and which had cowpats within the sample square, had higher earthworm biomass ($z = 2.25$, $P < 0.05$) and biomass of other potential badger food ($z = 5.98$, $P < 0.001$) compared with samples taken randomly in the same biotope.

The home ranges varied much in size, from 101 to 1489 ha. Male badgers had larger home ranges than females in spring ($z = 2.22$, $P < 0.05$), but no difference was found in autumn. Male ranges decreased while female ranges increased. from spring to autumn (Tab. 4).

Table 3. Total biomass and earthworm biomass found in hand-sorted soil samples taken in a boreal forest area in Malvik, central Norway

	Total biomass $g/m^2 \pm SE$	% earthworms of total biomass	n
Deciduous forest	100.2 ± 11.7	99.7	36
Pasture	65.8 ± 6.9	97.0	36
Rich coniferous forest	56.9 ± 9.1	99.6	36
Arable land	27.3 ± 5.6	98.2	36
Poor coniferous forest	2.1 ± 1.7	85.7	36
Fen	0.5 ± 0.2	20.0	36
Cowpat on pasture	168.9 ± 17.8	65.5	18

Table 4. Badger home ranges in spring and autumn, from a boreal forest area in Malvik, central Norway. M = male and F = female, * no data

		Home range size (ha)		
Badger no.	Age (years)	Spring	Autumn	Change
F1	4	209	292	+83
F2	3	152	348	+196
F3	1	168	302	+134
M1	5	725	466	–259
M2	4	1 489	627	–862
M3	1	531	284	–247
F4	3	251	*	*
F5	2	224	*	*
M4	2	*	170	*
M5	0	*	101	*
F6	9	*	124	*

There was no significant difference in the biotope composition of the home ranges between seasons ($\Lambda = 0.690$, $P = 0.80$, $n = 11$). The home range selection made by badgers within the study area was clearly not a random one ($\chi^2 = 28.64$, $df = 5$, $P < 0.001$). They used biotopes in the following order: deciduous forest > pasture > arable land > rich coniferous forest > fen > poor coniferous forest. There was no detectable difference between the three top-ranking biotopes (t's all <1.9, df = 10, P's all >0.05), but there was a clear contrast between those and the lower ranking ones (t's all > 2.9, df = 10, P's all <0.05).

When fixes were compared with home ranges, a difference in biotope use within home ranges was found between spring and autumn ($\Lambda = 0.132$, $P = 0.03$, $n = 11$). The only biotope showing any significant seasonal effect was pasture ($F_{1,9} = 6.47$, $P = 0.032$). Biotope use was not random, either in spring (8 animals, $\chi^2 = 21.80$, df = 5, $P < 0.001$) or autumn (9 animals, $\chi^2 = 19.84$, df = 5, $P < 0.005$). In spring, the ranking of biotopes in order of use was: deciduous forest > rich coniferous forest > poor coniferous forest > arable land > pasture > fen. Deciduous forest was used significantly more than the other biotopes in spring (t's all ≥ 3.00, df = 7, P's all < 0.05). The ranking in biotope use in autumn was: pasture > deciduous forest > arable land > poor coniferous forest > rich coniferous forest > fen, with no significant difference between the three top-ranking biotopes (t's all < 1.6, df = 8, P's all > 0.10), but there was a clear contrast between those and the lower ranking ones (t's all ≥ 2.53, df = 8, P's all < 0.05).

The group territories varied from 203 to 910 ha (Fig. 2, Tab. 5), but showed no correlation with the area of deciduous forest ($r = 0.01$, $P = 0.50$, $n = 4$). Territories increased in size as the number of deciduous forest patches increased ($r = 0.99$, $P < 0.01$, $n = 4$) at the same time as mean size of deciduous forest patches decreased ($r = -0.95$, $P < 0.05$, $n = 4$). Dispersion of deciduous forest patches accounted for much of the observed variation in territory size ($r^2 = 0.90$, $P = 0.05$, $n = 4$, Fig. 3).

Fig. 2. Territories of four adjacent badger groups and dispersion of deciduous forest patches (black areas), in a boreal forest area of central Norway. (A1–A4 refers to territories in Tab. 5)

Table 5. Territory size, amount of deciduous forest, number of deciduous forest patches and mean dispersion of deciduous forest patches within badger group territories in Malvik, central Norway

Territory	Number of badgers	Territory size (ha)	Amount of deciduous forest (ha)	Number of patches	Dispersion of patches (m)
A1	3	203	15.4	7	377
A2	3	368	22.1	15	688
A3	1	678	14.7	22	1 134
A4	3	910	18.8	33	1 137

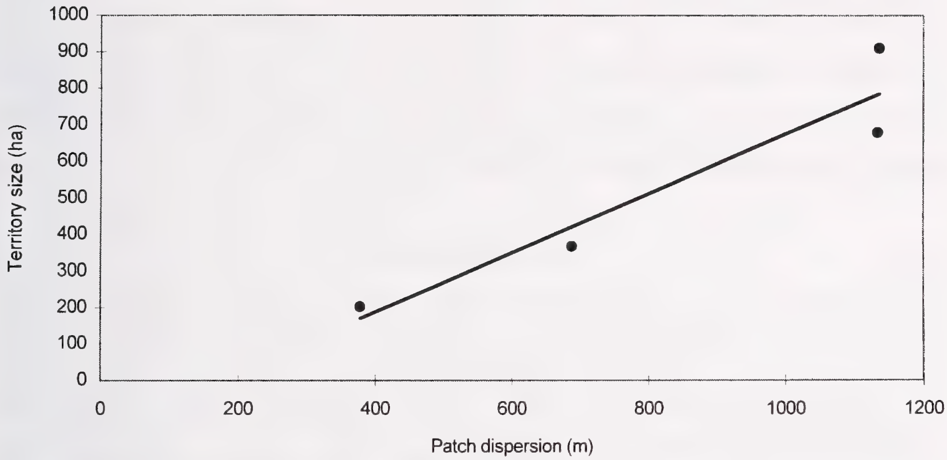


Fig. 3. Dispersion of deciduous forest patches accounted for 90% of the observed variation in territory size for badgers living in a boreal forest area in central Norway ($r^2 = 0.90$, $P = 0.05$)

Discussion

Dispersion of deciduous forest patches accounted for 90% of the observed variation in badgers territory size in the study area, even though the territories showed considerable variation in size and were huge compared to what is found in many other populations (reviewed in Woodroffe and Macdonald 1993). Earlier studies of badger populations living in more earthworm-rich habitats in the British Isles have shown that dispersion of important food patches can indicate the size of badger territories and that badgers adjust the confguration of their ranges in accordance with these earthworm-rich patches (Kruuk and Parish 1982; Silva et al. 1993), but such informations have been lacking from badgers living in a boreal habitat.

Recently, evidence has been put forward indicating that in some populations available sett sites can affect the spatial organization of badgers (Doncaster and Woodroffe 1993; Roper 1993). However, in the boreal forest of central Norway, where a territory on average contains twelve different setts (own unpubl. data), this seems less likely.

In the boreal forest studied, where large coniferous forest areas containing few earthworms surround the agricultural land and the deciduous forest that is rich in earthworms, badgers prefer to forage in biotopes with high earthworm biomass both in spring and autumn. We found no increased utilization of poor coniferous forest nor any large quantities of berries in the diet in autumn, as shown in earlier studies from the boreal forest at

Grimsö, south-central Sweden (Seiler et al. 1995; E. Lindström pers. comm.). Although utilization of poor coniferous forest increased during the autumn at Grimsö, earthworm-rich biotopes were still most used (E. Lindström pers. comm.). One possible explanation of the observed differences between the two boreal areas might be that earthworms were so readily available and numerous during the year of our study that the badgers did not eat berries (Shepherdson et al. 1990).

However, although no increased utilization of poor coniferous forest was found, badgers increased their utilization of pasture in autumn. In Scotland Kruuk (1989) found that badgers used places with high accumulations of sheep faeces as foraging patches. Such accumulations of faeces from domestic animals concentrate the availability and increase the predictability of earthworms (Lee 1985), thus making pasture a profitable biotope for badgers to forage at this time of year.

In spring resident males make extra-territorial movements and it is not uncommon with extra-group matings (Evans et al. 1989). Such behaviour can explain why male badgers in the boreal forest of central Norway had larger home ranges than females in spring. In our study area, where large poor coniferous forest areas surround the more utilizated biotopes rich in earthworms, there are probably good possibilities for male badgers to roam over large areas, searching for receptive females.

Acknowledgements

We are grateful for the financial support given by the NINA institute program on landscape ecology, the County Governor's office for environmental affairs in Sør-Trøndelag and the University of Trondheim. We would like to thank John Atle Kålås and Jon E. Swenson for useful comments on earlier drafts of this manuscript, and the North European badger group for helpful collaboration over many years. We also thank Torgrim Sund from Asplan Viak and the Sør-Trøndelag County Agricultural and Forestry Office for help to prepare the digitized polygon map, and the veterinary surgeon, Ingolf Hansen, for implanting the radio transmitters. We are indebted to Richard Binns for improving the English, and Andreas Seiler for help with the Zusammenfassung.

Zusammenfassung

Räumliche Organisation und Habitatnutzung von Dachsen (Meles meles): Verteilung der Nahrungsbiotope im borealen Mittelnorwegen.

Der Einfluß von Nahrungsangebot auf die Habitatnutzung sowie auf Streifgebiets- und Reviergröße von Dachsen (*Meles meles* L.) wurde über einen Zeitraum von acht Monaten im borealen, landwirtschaftlich geprägten Mittelnorwegen studiert. Die Nahrung bestand sowohl im Frühling als auch im Herbst vorwiegend aus Regenwürmern. Beeren spielten nur eine untergeordnete Rolle während des Herbstes. Das Vorkommen von Regenwürmern war sehr fleckenhaft, die größte Biomasse fand sich in Laubwaldbiotopen. Hohe Regenwurmdichten fanden sich ebenfalls unter Kuhfladen in den Weidegebieten, wodurch die Biomasse und die Vorhersagbarkeit von potentieller Dachsnahrung erhöht wurde. Zwischen Frühling und Herbst fand sich kein Unterschied in der Biotopzusammensetzung der Streifgebiete, allerdings wurden die Biotope in unterschiedlicher Weise genutzt. Laubwaldbiotope wurden das ganze Jahr über stark genutzt, Weideflächen hingegen vorwiegend im Herbst. Die Verteilung von Laubwaldbiotopen in den Gruppenrevieren hatte deutlichen Effekt auf die Größe der Streifgebiete.

References

Aebischer, N. J.; Robertsen, P. A.; Kenward, R. E. (1993 a): Compositional analysis of habitat use from radio-tracking data. Ecology **74**, 1313–1325.

AEBISCHER, N. J.; ROBERTSEN, P. A.; KENWARD, R. E. (1993 b): Survival and habitat utilisation: a case for compositional analysis. In: Marked individuals in the study of bird population. Ed. by J. D. LEBRETON and P. M. NORTH. Basel: Birkhäuser Verlag. Pp. 343–353.

AHNLUND, H. (1976): Age determination in the European badger, *Meles meles* L. Z. Säugetierkunde **41**, 119–125.

BEVANGER, K.; LINDSTRÖM, E. (1995): Distributional history of the European badger *Meles meles* in Scandinavia during the 20th century. Ann. Zool. Fennici. **32**, 5–9.

BURROUGH, P. A. (1986): Principles of geographical information systems for land resources assessment. Oxford: Clarendon Press.

CHEESEMAN, C. L.; MALLINSON, P. J. (1980): Radio tracking in the study of bovine tuberculosis in badgers. In: A handbook on biotelemetry and radio tracking. Ed. by C. J. AMLANER and D. W. MACDONALD. Oxford: Pergamon Press. Pp. 649–656.

CHEESEMAN, C. L.; JONES, G. W.; GALLAGHER, J.; MALLINSON, P. J. (1981): The population structure, density and prevalence of tuberculosis (*Mycobacterium bovis*) in badgers (*Meles meles*) from four areas in south-west England. J. Appl. Ecol. **18**, 795–804.

CHEESEMAN, C. L.; WILESMITH, J. W.; RYAN, J.; MALLINSON, P. J. (1987): Badger population dynamics in a high density area. Symp. Zool. Soc. (London) **58**, 279–294.

DAVIES, N. B. (1991): Mating systems. In: Behavioural ecology: an evolutionary approach. 3rd ed. Ed. by J. R. KREBS and N. B. DAVIES. Oxford: Blackwell Scientific Publ. Pp. 263–294.

DONCASTER, C. P.; WOODROFFE, R. (1993): Den site can determine shape and size of badger territories: implications for group-living. Oikos **66**, 88–93.

EDWARDS, C. A.; LOFTY, J. R. (1977): Biology of earthworms. London: Chapman and Hall.

ESRI (1990): PC ARC/INFO (Software, Version 3.4D). California, Redlands: Environmental Systems Research Institute inc.

ESRI (1992): ArcView (Software). California, Redlands: Environmental Systems Research Institute inc.

EVANS, P. G. H.; MACDONALD, D. W.; CHEESEMAN, C. L. (1989): Social structure of the Eurasian badger (*Meles meles*): genetic evidence. J. Zool. (London) **218**, 587–595.

FOWLER, P. A.; RACEY, P. A. (1988): Overwintering strategies of the badger, *Meles meles*, at 57 °N. J. Zool. (London) **214**, 635–651.

FREMSTAD, E.; ELVEN, R. (1987): Enheter for vegetasjonskartlegging i Norge. Økoforsk utred. 1987: 1. Trondheim: Økoforsk, NAVF. (in Norwegian)

HARRIS, S.; CRESSWELL, W. J.; FORDE, P. G.; TREWHELLA, W. J.; WOOLLARD, T.; WRAY, S. (1990): Home-range analysis using radio-tracking data – a review of problems and techniques particularly as applied to the study of mammals. Mammal Rev. **20**, 97–103.

HASLETT, J. R. (1990): Geographic Information Systems: a new approach to habitat definition and the study of distributions. Trends Ecol. Evol. **5**, 214–218.

KENWARD, R. E. (1990): Ranges IV. Software for analysing animal location data. Wareham, UK: Institute of Terrestrial Ecology.

KORSCHGEN, L. J. (1980): Procedures for food-habits analyses. In: Wildlife investigational techniques manual. Ed. by S. D. SCHEMNITZ. Washington D.C.: The Wildlife Society. Pp. 113–137.

KRUUK, H. (1978): Foraging and spatial organisation of the European badger, *Meles meles* L. Behav. Ecol. Sociobiol. **4**, 75–89.

KRUUK, H. (1989): The social badger: ecology and behaviour of a group-living carnivore (*Meles meles*). Oxford: Oxford Univ. Press.

KRUUK, H.; MACDONALD, D. W. (1985): Group territories of carnivores: empires and enclaves. In: Behavioural ecology: ecological consequences of adaptive behaviour. Ed. by R. M. SIBLY and R. H. SMITH. Oxford: Blackwell Scientific Publ. Pp. 521–536.

KRUUK, H.; PARISH, T. (1981): Feeding specialization of the European badger *Meles meles* in Scotland. J. Anim. Ecol. **50**, 773–788.

KRUUK, H.; PARISH, T. (1982): Factors affecting population density, group size and territory size of the European badger, *Meles meles*. J. Zool. (London) **196**, 31–39.

LEE, K. E. (1985): Earthworms: their ecology and relationships with soils and land use. Sydney: Academic Press.

LINDSTRÖM, E. (1989): The role of medium-sized carnivores in the Nordic boreal forest. Finnish Game Res. **46**, 53–63.

LÜPS, P.; ROPER, T. J.; STOCKER, G. (1987): Stomach contents of badgers (*Meles meles* L.) in central Switzerland. Mammalia **51**, 559–569.

Macdonald, D. W. (1983 a): The ecology of carnivore social behaviour. Nature **301**, 379–384.
Macdonald, D. W. (1983 b): Predation on earthworms by terrestrial vertebrates. In: Earthworm ecology. Ed. by J. E. Satchell. London: Chapman and Hall. Pp. 393–414.
Martín, R.; Rodriguez, A.; Delibes, M. (1995): Local feeding specialization by badgers (*Meles meles*) in a Mediterranean environment. Oecologia **101**, 45–50.
Mellgren, R. L.; Roper, T. J. (1986): Spatial learning and discrimination of food patches in the European badger (*Meler meles* L.). Anim. Behav. **34**, 1129–1134.
Neal, E. (1986): The natural history of badgers. London: Croom Helm.
Neal, E. (1988): The stomach contents of badgers, *Meles meles*. J. Zool. (London) **215**, 367–369.
Pigozzi, G. (1991): The diet of the European badger in a Mediterranien costal area. Acta theriol. **36**, 293–306.
Rodríguez, A.; Delibes, M. (1992): Food habits of badgers (*Meles meles*) in an arid habitat. J. Zool. (London) **227**, 347–350.
Rodríguez, A.; Martín, R.; Delibes, M. (1996): Space use and activity in a mediterranean population of badgers *Meles meles*. Acta theriol. **41**, 59–72.
Roper, T. J. (1993): Badger setts as a limiting resource. In: The badger. Ed. by T. J. Hayden. Dublin: Royal Irish Academy. Pp. 24–34.
Roper, T. J. (1994): The European badger *Meles meles*: food specialist or generalist? J. Zool. (London) **234**, 437–452.
Seiler, A.; Lindström, E.; Stenström, D. (1995): Badger abundance and activity in relation to fragmentation of forarging biotopes. Ann. Zool. Fennici **32**, 37–45.
Shepherdson, D. J.; Roper, T. J.; Lüps, P. (1990): Diet, food availability and foraging behavior of badgers (*Meles meles* L.) in southern England. Z. Säugetierkunde **55**, 81–93.
Silva, J. da; Macdonald, D. W.; Evans, P. G. H. (1994): Net costs of group living in a solitary forager, the Eurasian badger (*Meles meles*). Behav. Ecol. **5**, 151–158.
Silva, J. da; Woodroffe, R.; Macdonald, D. W. (1993): Habitat, food availability and group territoriality in the European badger, *Meles meles*. Oecologia **95**, 558–564.
Skoog, P. (1970): The food of the Swedish badger, (*Meles meles* L). Viltrevy **7**, 1–120.
SPSS Inc. (1993): SPSS for Windows: Release 6.0 (Software). Chicago: SPSS Inc.
Woodroffe, R.; Macdonald, D. W. (1993): Badger sociality – models of spatial grouping. Symp. Zool. Soc. (London) **65**, 145–169.

Authors' addresses: Henrik Brøseth and Dr. scient. Kjetil Bevanger, Norwegian Institute for Nature Research, Tungasletta 2, N-7005 Trondheim, Norway; Bård Knutsen, Tyttebærveien 2, N-7550 Hommelvik, Norway.

Z. Säugetierkunde **62** (1997) 23–29

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Nesting and digging behavior in two rodent species (*Akodon azarae* and *Calomys laucha*) under laboratory and field conditions

By Karina Hodara, Olga Virginia Suárez, and F. O. Kravetz

Departamento de Biología, Universidad de Buenos Aires, Buenos Aires Argentina

Receipt of Ms. 15. 03. 1995
Acceptance of Ms. 19. 09. 1996

Abstract

Nesting and digging habits as well as shelter locations were studied in *Akodon azarae* and *Calomys laucha* under laboratory conditions. Shelter locations were compared with burrow and nest locations in the field. Laboratory results showed that *A. azarae* built more burrows than surface nests while *C. laucha* built both surface nests and burrows and both species selected sods from external borders of cropfields (area out of the wire fences characterized by the most compacted soils and abundant plant cover) for building their shelters. Field observations showed that both *A. azarae* and *C. laucha* used burrows. In the field *A. azarae* shelters were located in the internal borders of cropfields (habitat with heavy plant cover placed under wire fences), while those of *C. laucha* were found in cropfields (the most perturbed habitat). We conclude that nesting and digging behavior in the laboratory reflects only soil selection while in the field it is also affected by interspecific competition, which causes spatial segregation of shelter locations between the two species.

Introduction

Akodon azarae and *Calomys laucha* are two of the most abundant murid rodent species that inhabit pampean agrarian ecosystems of central Argentina. Previous studies (Kravetz et al. 1981; Kravetz and Polop 1983; Busch et al. 1984; Mills et al. 1991; Busch and Kravetz 1992 a) suggest that these species show a differential habitat use. Rodents are distributed between two main macrohabitats: cropfields and their borders (marginal weedy areas below wire fences). While *Akodon azarae* uses more frequently cropfield borders, *Calomys laucha* occupies both habitats, but it is more abundant in the cropfields.

This spatial distribution is maintained, among other factors, by interference competition, *A. azarae* being competitively dominant over *C. laucha* (Busch and Kravetz 1992 a). In removal experiments, Busch and Kravetz (1992 b) demonstrated that the larger species, *A. azarae*, limited the abundance of *C. laucha* in the borders, and behavioral studies showed that competitive interference between both species may be expressed in spatial segregation produced from individual interactions (Busch and Kravetz 1992 b; Cueto et al. 1995).

In heterogeneous environments, habitat selection can exert marked effects on the outcome of interspecific interactions (Rosenzweig 1979; Pimm et al. 1985; Bowers and Dooley 1991; Danielson 1991), and differential habitat selection is considered one of the principal relationships that permit species to coexist (Rosenzweig 1981).

Evidences of direct methods as nesting and digging habits and the spatial location of the shelters (Kotler 1985) may contribute to elucidate the determinants of habitat choice and habitat occupancy patterns.

The aim of this work is to study the choice of habitat for nesting and digging habits in *Akodon azarae* and *Calomys laucha* under two situations: 1) Laboratory conditions (excluding intra- and interspecific competition) and 2) Natural conditions in the field.

Material and Methods

Laboratory experiments

Between August and December 1992, we studied habitat selection and the kind of shelters constructed by *A. azarae* and *C. laucha*. The experiment was conducted with 14 overwintering adult animals of *A. azarae* and 14 of *C. laucha* (7 females and 7 males in each case), which were caught in Diego Gaynor (34° 08′ S, 59° 14 W, Buenos Aires Province, Argentina) with Sherman live traps. Diego Gaynor is located in the Pampean region, the climate is temperate, and is characterized by agriculture and cattle farming. The landscape is composed of individual cropfields surrounded by wire fences with borders dominated by weedy species.

All mice were acclimated to laboratory conditions for two months before the experiment began. The animals were individually kept in laboratory cages (0.35 by 0.28 by 0.15 m) provided with sunflower seeds, water ad libitum and wood shavings as bedding materials. All individuals were maintained under a daily cycle of 14 h light: 10 h dark, an ambient temperature at 20 ± 4 °C and 60–80% of humidity.

The test apparatus used was a three glass boxes system (0.30 by 0.30 m side by 0.20 m high each box) connected with three equidistant wirework tubes (1.0 m long and 5 cm diameter each tube) (Fig. 1).

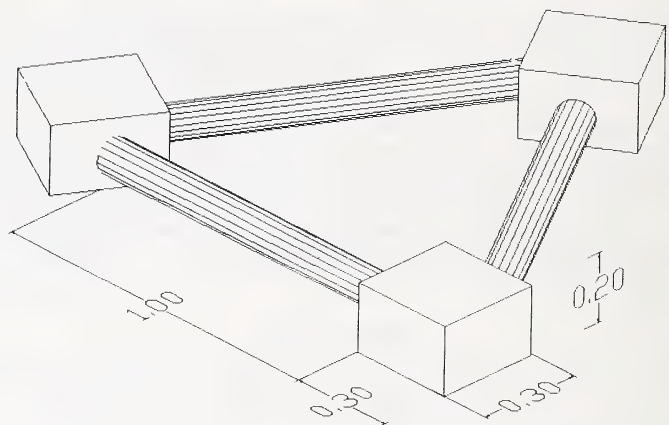


Fig. 1. A three glass box system connected with equidistant tubes used for laboratory experiences.

In each box one sod was used as substrate representing one of the three soil types being studied:

Soil type A: Cropfield characterized by a soil poorly compacted and strongly disturbed by agricultural activities.

Soil type B: Internal border (under wire fences limiting the cropfields) represented by strong and relatively stable plant cover and less compacted soil than the external one.

Soil type C: External border (out of the wire fences) characterized by abundant vegetation cover (with creeping species and rhizoma plants) and soil highly compacted by cattle.

Sods (0.30 by 0.30 m size by 0.15 m high each one) were taken out from D. Gaynor locality. Plant cover of types B and C sods were reaped at 0.10 m high previously to be placed into glass boxes. A water bottle and a supply of 50 g of oat seeds were offered into each box. Same conditions of day length, temperature and humidity were maintained previously and during the experiments.

Procedure

The animals were individually placed into the experimental system during 4 consecutive days. Each individual was randomly assigned to one box when it was introduced into the system. Observations started after 24 h of acclimatization to the experimental apparatus and they were initiated 2–3 h before the beginning of the dark period. There were two observations of 15 min per day. After each experiment the sods were removed and replaced by new ones; food and water were changed and the boxes were washed.

During each experiment we recorded:
Total permanence time: Total time (in min) spent by each animal in each habitat (Cropfield, internal border or external one).
Habitat types selectioned for building shelters.
Types of shelters built. They could be burrows (in deepness) or nests (at surface).

Field observations

The study was carried out during August 1993 on one 1.2 ha grid in a sunflower cropfield and its adjacent border in D. Gaynor locality. The experimental plot consisted of 120 Sherman live trap stations spaced at 10 m intervals.

From captured animals, all overwintering adult individuals (12 of *A. azarae* and 10 of *C. laucha*) were tracked using fluorescent pigments (Lemen and Freeman 1985), in order to determine their shelter locations. Selected animals were placed into a plastic bag containing a small amount of fluorescent pigment (Radiant Color, Richmond, CA), gently shaken and released at the site of capture. Animals covered with the pigment left a trail that could be followed at night with a longwave ultraviolet-light source locating shelters and identifying the type of shelter used and the habitat where it was placed.

Statistics

Kruskal-Wallis one-way analysis of variance was used to compare permanence times among habitat types. Dunn test for multiple non-parametric comparisons were performed if differences in permanence time were statistically significant (Siegel 1989). In order to compare the frequencies of types of shelters built and types of habitats selected we performed binomial tests (with grouped and ungrouped categories, Sokal and Rohlf 1980). In the first case the probabilities under the null hypothesis of random construction where $p = q = 0.5$, while in the second case the null hypothesis of random selection was $p = 0.33$ and $q = 0.67$. Fisher's exact probability test (Siegel 1989) was made for post-hoc analysis between laboratory and field results for both species. Values of $P < 0.05$ were considered to be significant in all analysis, except in Dunn multiple comparsions where the significant level was fixed at $P < 0.10$.

Results

Laboratory observations

Table 1. Total permanence time in each glass box. Time measures are in minutes (Median values are in parentheses).

	Species	
	A. azarae	*C. laucha*
Sod A	124 (0.5)	279.5 (2.5)
Sod B	473 (12.5)	217.5 (0)
Sod C	663* (56)	763* (69)
Total	1 260	1 260

Sods A, B and C: Sods from soil types A, B and C respectively. * Significantly different ($P < 0.05$ Kruskal-Wallis one-way analysis of variance).

In both species, individuals stayed significantly longer times in the soil type C (external border) than in the other 2 soil types (H: 6.00, $df = 2$, $P < 0.05$, Dunn $P < 0.10$ for *A. azarae* and H: 6.48, $df = 2$, $P < 0.05$, Dunn $P < 0.10$ for *C. laucha*) (Tab. 1).

Soil type C was also selected more frequently than the other types by *A. azarae* and *C. laucha* individuals for building their shelters (P(13): 0.008, $n = 22$, $P < 0.01$) and (P(10): 0.003, $n = 14$, $P < 0.01$), respectively (Tab. 2). Some *A. azarae* individuals built more than one shelter ($n = 22$) but all individuals of *C. laucha* built only one shelter ($n = 14$).

However, the kind of shelters built different according to the species. *A. azarae* built significantly more burrows in depth than surface nests (P(19): 0.0003, $n = 22$, $P < 0.01$), whereas *C. laucha* built surface nests as frequently as burrows (P(8): 0.183, $n = 14$, $P > 0.05$) (Tab. 3).

Table 2. Sod selection for building the shelters under laboratory conditions.

Species	Number of individuals	Number of observations	Number of shelters in each soil type		
			Sod A	Sod B	Sod C
A. azarae	14	22	2	7	13 **
C. laucha	14	14	0	4	10 **

Sods A, B and C: Sods from soil types A, B and C respectively.
** Significantly different ($P < 0.01$ Binomial test with grouped categories).

Table 3. Shelter types built under laboratory conditions

Species	Number of observations	Number of shelters	
		Burrows	Nests
A. azarae	22	19 **	3
C. laucha	14	6	8

** Significantly different ($P < 0.01$ Binomial test).

Surface nests were built with cut dry grasses delicately woven, as covered nests, and were placed in shallow depressions. They were cup-shaped nests with sides and a cover and they measured up to 5–6 cm in diameter for *C. laucha* and 8–10 cm for *A. azarae*.

Burrow systems of *A. azarae* had a branching structure. All burrows had a single nest chamber, packed with dry grasses and a variable number of tunnels to the surface. Rests of seeds and dry grasses in the central chamber and in the tunnels were observed in some cases.

Field results

According to fluorescent trails, burrows of *A. azarae* were located more frequently in the internal border ($P(8)$: 0.014, $n = 12$, $P < 0.05$) while *C. laucha* shelters were more frequently placed in the cropfield ($P(8)$: 0.002, $n = 10$, $P < 0.01$) (Tab. 4).

In agreement with laboratory observations *A. azarae* used burrows more frequently than surface nests in the field ($P(12)$: 0.0002, $n = 12$, $P < 0.01$). However, *C. laucha* used significantly more burrows than surface nests in the field ($P(9)$: 0.009, $n = 10$, $P < 0.01$) differing with laboratory observations (Tab. 5).

Table 4. Distribution of shelters in the 3 soil types under field conditions

Species	Number of individuals	Number of shelters in each soil type		
		Cropfield	Internal border	External border
A. azarae	12	4	8 *	0
C. laucha	10	8 **	2	0

* Significantly different ($P < 0.05$ Binomial test with grouped categories).
** Significantly different ($P < 0.01$ Binomial test with grouped categories).

Table 5. Shelter types located by marked animals under field conditions

Species	Number of individuals	Number of shelters	
		Burrows	Nests
A. azarae	12	12 **	0
C. laucha	10	9 **	1

** Significantly different (P < 0.01 Binomial test).

Shelter locations did not significantly differ under laboratory and field conditions for *A. azarae* (Fisher's exact test, P = 0.154), while *C. laucha* shelters were more frequently located in cropfields under field conditions, and in the external border in the laboratory (Fisher's exact test, P = 0.0001).

Discussion

According to our results, *A. azarae* individuals selected cropfield borders for building their burrows, both under laboratory and field conditions. However, in the first case the external border was more used, while under field conditions burrows were located in the internal border. The higher abundance of *A. azarae* in borders relative to cropfields is well documented (Mills et al. 1991; Busch and Kravetz 1992 a), but it is the first study in which it is confirmed that individuals of this species select borders for locating their burrows, thus these habitats are probaly the center of their daily activities and reproductive sites. The choice of a site for shelter location may be influenced by a number of factors, many of them being absent under laboratory conditions. Whether the selection is the same under such different circumstances, may depend on which keys animals use in order to identify a habitat. According to the theory of habitat selection, individuals may select those habitats where fitness is maximized (Morris 1987, 1988), assuming that animals are completely acknowledged with respect to the relative fitness rewards of different habitats. Habitat selection should be evolved through the identification of certain habitat cues, that bring out indirect information about these potential fitness rewards. In our case, which are the main features of each habitat that may be affecting its selection? From previous works (Bonaventura et al. 1989, 1992), it is clear that *A. azarae* abundance is correlated with high plant cover, which is found in both types of cropfield borders (external and internal one). However the borders are still selected in the laboratory, where plant cover was reaped at 10 cm high. The strongest difference between sods of different habitats are the characteristics of the soil. That from the external border is the most compacted soil, and apparently is the best fit to dig burrows, especially those of *A. azarae*, with a branching structure that needs the construction of tunnels. Cropfields soil is poorly structured due to plowing, and it was frequently disrupted when we tried to take out a sod, and the internal border soil is slightly less structured that the external one.

The selection of borders may then be related to both the presence of a good plant cover (under field conditions), that confers refuge from predators; and to soil characteristics, that favors burrow construction (under field and laboratory conditions). The difference between the relative use of external and internal borders under laboratory and field conditions must be related to the effect, in the first case, of only soil characteristics, while in the fields there are others factors, such as trampling by cattle, that may disturb more the external border than the internal one.

C. laucha located their nests and burrows in the borders under laboratory conditions, but it used the cropfield more in the field. This species shows more similar abundance in

the two habitats than *A. azarae*, although it is generally more often captured in cropfields than in borders (Mills et al. 1991; Busch and Kravetz 1992 a). Habitat segregation between these two species has been attributed to interspecific competition, which causes a shift in *C. laucha* towards cropfields (Busch and Kravetz 1992 b), and competitive dominance of *A. azarae* over *C. laucha* was also observed by Cueto et al. (1995) with respect to the access to food resources.

Our work provides another evidence that the apparent preference of *C. laucha* for cropfields, observed in natural conditions, may be caused by interspecific competition with *A. azarae*; since solitary individuals in laboratory, select sods of borders to build shelters and remain longer times in this type of habitat.

With respect to nesting and digging habits, *A. azarae* dug burrows and *C. laucha* built surface nests and burrows in the laboratory, while in the field both species used burrows. According to laboratory results, *A. azarae* probably uses burrows dug by its own, while *C. laucha* may occupy cracks and little modificated holds as burrows in the cropfields under field conditions, as observed by Busch et al. (1984) or dig own burrows as was demonstrated by Yunes et al. (1991). Living in an underground nest could be an adaptive response by *C. laucha* to avoid avian predators in cropfields where the plant cover is scarce, such as at harvest time or when the cropfields are recently tilled, and to survive at low temperatures, as was postulated by Kravetz et al. (1981) and Yunes et al. (1991).

The results of the present study suggest that *A. azarae* has the resident conditions in borders, which have the best habitability and limits the access of *C. laucha* to these habitats.

Therefore, *C. laucha* reduces direct competition with *A. azarae* in the field by moving to the cropfields that are less preferred habitats, because of being highly disturbed by agricultural activities and having low plant cover. The use of burrows may be favored in this kind of habitats instead of the more exposed surface nests. The ability of *C. laucha* to exploit unstable temporarily suitable habitats, such as the cropfields (Mills et al. 1991) which are less often occupied by *A. azarae*, is in agreement with previous studies indicating that habitat shift is an adaptive behavior for subordinate species in two-species competitive system (Rosenzweig 1979).

In summary, we observed that *A. azarae* uses the most suitable habitat both under field and laboratory conditions, while *C. laucha* shifts its habitat use from the borders, when *A. azarae* is absent, and to the less suitable habitat when this species is present.

Acknowledgements

We thank D. Gaynor personnel for their assistance in the field work. We also thank Dr. M. Busch and Lic. G. Cueto for critically reviewing the manuscript. A. Sartori provided invaluable help during field trapping periods and Dr. M. Giurfa translated the German summary. This work was funded by grants from CONICET (Argentina).

Zusammenfassung

Nestbau- und Grabverhalten zweier Nagetierarten (Akodon azarae und Calomys laucha) unter Labor- und Feldbedingungen

Es wurden Verhaltensweisen beim Nestbau- und Grabverhalten sowie die Verteilung der Unterschlupfe von *Akodon azarae* und *Calomys laucha* unter Laborbedingungen untersucht. Die Lage der Unterschlupfe wurde dann mit der Lage der Erdhöhlen und Nester auf dem Feld verglichen. Die im Labor erzielten Resultate zeigten, daß *A. azarae* mehr Erdlöcher als Nester an der Oberfläche gebaut hatte, während *C. laucha* sowohl Nester an der Oberfläche, als auch Erdlöcher gebaut hatte. Beide Arten wählten Feldstücke vom äußeren Rand des Getreidefeldes (Standorte ohne Drahtzaun, mit am stärksten verdichteten Boden und einer artenreichen Pflanzendecke). Die Feldbeobachtungen ergaben, daß

A. azarae und *C. laucha* Erdhöhlen nutzten. Die Unterschlupfe von *A. azarae* befanden sich an den Innenrändern des Getreidefeldes (Standort unter einem Drahtzaun mit einer dichten Pflanzendecke), die von *C.laucha* jedoch befanden sich im Getreidefeld (Standort mit den meisten Störungen). Wir folgern hieraus, daß das Nestbau- und Grabverhalten im Labor nur von der Auswahl des Untergrundes abhängt. Auf dem Feld wird es hingegen auch durch interspezifische Konkurrenz beeinflußt, was eine räumliche Trennung der Aufzuchtgebiete beider Spezies zur Folge hat.

References

Bonaventura, S. M.; Kravetz, F. O. (1989): Relación roedor-vegetación: importancia de la disponibilidad de cobertura verde para *Akodon azarae* durante el invierno. Physis **47**, 1–5.

Bonaventura, S. M.; Kravetz, F. O.; Suarez, O. V. (1992): The relationship between food availability, space use and territoriality in *Akodon azarae* (Rodentia, Cricetidae). Mammalia **56**, 407–416.

Bowers, M. A.; Dooley, J. L. Jr. (1991): Landscape composition and the intensity and outcome of two species competition. Oikos **60**, 180–186.

Busch, M.; Kravetz, F. O.; Percich, R. E.; Zuleta, G. A. (1984): Propuestas para un control ecológico de la Fiebre Hemorrágica Argentina a través del manejo del hábitat. Medicina (Buenos Aires). **44**, 34–40.

Busch, M.; Kravetz, F. O. (1992 a): Competitive interactions among rodents (*Akodon azarae, Calomys laucha, C. musculinus* and *Oligoryzomys flavescens*) in a two habitat system. I. Spatial and numerical relationships **56**, 45–56.

Busch, M.; Kravetz, F. O. (1992 b): Competitive interactions among rodents *(Akodon azarae, Calomys laucha, C. musculinus* and *Oligoryzomys flavescens*) in a two habitat system. II. Effect of species removal. Mammalia **56**, 541–554.

Cueto, G. R.; Bilenca, D. N.; Kravetz, F. O. (1995): Interspecific social relationships in three murid rodent species of central Argentina, after fasting and unlimited food. Behaviour **132**, 811–820.

Danielson, B. J. (1991): Communities in a landscape: the influence of habitat heterogeneity on the interactions between species. Am. Nat. **138**, 1105–1120.

Kotler, B. P. (1985): Microhabitat utilization in desert rodents: a comparison of two methods of measurement. J. Mammalogy **66**, 374–378.

Kravetz, F. O.; Manjon, M. C.; Busch, M.; Percich, R. E.; Marconi, P.; Torres, M. (1981): Ecología de *Calomys laucha* (Rodentia, Cricetidae) en el Departamento de Río Cuarto (Córdoba). I. Dinámica de población. Ecología (Argentina) **6**, 15–22.

Kravetz, F. O.; Polop, J. J. (1983): Comunidades de roedores en agroecosistemas del Departamento de Río Cuarto, Córdoba. Ecosur **10**, 1–10.

Lemen, C. A.; Freeman, P. W. (1985): Tracking mammals with fluorescent pigment: a new technique. J. Mammalogy **66**, 134–136.

Mills, J. N.; Ellis, B. A.; McKee, K. T. Jr.; Maiztegui, J. I.; Childs, J. E. (1991): Habitat associations and relative densities of rodent populations in cultivated areas of central Argentina. J. Mammalogy **72**, 470–479.

Morris, D. W. (1987): Ecological scale and habitat use. Ecology **68**, 362–369.

Morris, D. W. (1988): Habitat-dependent population regulation and community structure. Evol. Ecol. **2**, 253–269.

Pimm, S. L.; Rosenzweig, M. L.; Mitchell, W. (1985): Competition and food selection: field tests of a theory. Ecology **66**, 798–807.

Rosenzweig, M. L. (1979): Optimal habitat selection in two-species competitive systems. Fortschr. Zool. **25**, 283–293.

Rosenzweig, M. L. (1981): A theory of habitat selection. Ecology **62**, 327–335.

Siegel, S. (1989): Non-parametric statistics for the behavioral science. New York: Mc Graw-Hill.

Sokal, R. R.; Rohlf, F. J. (1980): Biometry. San Francisco: W. H. Freedman.

Yunes, R. M.; Cutrera, R. A.; Castro Vazquez, A. (1991): Nesting and digging behavior in three species of *Calomys* (Rodentia: Cricetidae). Physiol. Behav. **49**, 489–492.

Authors' address: Lic. Karina Hodara, Lic. Olga v. Suarez, and Dr. Fernando O. Kravetz, Departamento de Ciencias Biológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Ciudad Universitaria, Pabellón II, 4° Piso. (1428) Buenos Aires, Argentina.

Z. Säugetierkunde **62** (1997) 30–36

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Space and time use in syntopic populations of *Akodon azarae* and *Calomys venustus* (Rodentia, Muridae)

By J. Priotto and J. Polop

Departamento de Ciencias Naturales, Universidad Nacional de Río Cuarto, Río Cuarto, Córdoba, Argentina

Receipt of Ms. 15. 01. 1996
Acceptance of Ms. 19. 09. 1996

Abstract

Spatial use and activity times were studied in syntopic populations of *Akodon azarae* and *Calomys venustus* in agroecosystems of southern Cordoba Province (Argentina). Space use was determined by recording co-occurrence of both species at the same trap station whereas activity times were obtained by means of traps fitted with timers that started at the animal capture. Data were analysed during reproductive and non-reproductive periods. Spatial co-occurrence of *A. azarae* with *C. venustus* was recorded in both periods. A separation between the species under study was observed in the niche temporal axis. *A. azarae* showed continuous activity with variational peaks depending on the reproductive and non-reproductive periods whereas *C. venustus* showed activity during crepuscular and night hours in both periods. Consequently, these differences in the times of resource use are likely to be the main mechanism for syntopic co-existence of *A. azarae* and *C. venustus*.

Introduction

In small-rodent communities inhabiting agroecosystems of southern Cordoba Province (Argentina), *Akodon azarae* and *Calomys venustus* are frequently captured in the same type of habitat (Kravetz and Polop 1983; Polop et al. 1985; Polop and Sabattini 1993). This seems to indicate that both populations are likely to have access to the same type of resources. However, an axiom of multidimensional niche theory (Hutchinson 1957) holds that each species will have a limited specificity, within a range, for each dimension. Thus, coexistence of *A. azarae* and *C. venustus* could be explained only to the extent in which each species uses the niche dimensions in a different way. *A. azarae* and *C. venustus* populations are characterized by seasonal density changes, annual turnover, iteroparous reproduction and cohort-specific reproductive tactics (Crespo 1966; Pearson 1967; Dalby 1975; Zuleta 1989; Polop 1996).

In studies on rodent communities, food not always seems to be limitative; for this reason it has been suggested that habitat differences would become the main mechanism to prevent interference competition (Schoener 1974; Meserve 1981). It is also assumed that coexistence between sympatric populations is given not only by segregation at the level of the niche spatial dimension but also by a separation at the level of the temporal dimension. Differences in the latter dimension seem to be the mechanism that best explains how to reduce interference competition (Carothers and Jaksic 1984; Canova 1993).

On the basis that the hypothesis of multidimensional niche (Hutchinson 1957) will explain coexistence between *A. azarae* and *C. venustus*, the aim of this study was to determine spatial use and activity time of these two species in agroecosystem habitats.

Material and methods

The study was carried out in Chucul (64° 20′ 09″ West, 32° 21′ 06″ South) Rio Cuarto Department, Cordoba Province, Argentina. Phytogeographically this region corresponds to the "Provincia del Espinal" "Distrito del Algarrobo" (Cabrera 1953). This is a plain at a low elevation (600–900 m) with vegetation dominated by algarrobo (*Prosopis alba, P. nigra*), accompanied by quebracho blanco (*Aspidosperma quebracho blanco*), mistol (*Zizyphus mistol*) and itin (*Portulaca kuntzie*). The vegetation, however, has undergone marked alterations as a result of agriculture and cattle farming. At present, the landscape mainly consists of individual cropfields, surrounded by wire fences with borders dominated by weedy species. In the area, the railway banks are an environment where some rodent populations reach high densities. Plant community is characterised by pasture interspersed with bushes. Despite the influence of nearby crop fields, it bears some resemblance with indigenous vegetation. This environment was selected for sampling.

Rodents were caught from April 1990 to February 1995 in traps arranged in a grid of 6×10 traps (50 m×90 m) with an interestation interval of 10 m per one Sherman live trap, placed in each station, baited with a mixture of peanut butter and cow fat. Monthly censuses were taken in periods of 5 successive days. Traps were checked daily in the morning.

Co-occurrence of the two species was recorded in the same trap station during the same sampling period to measure spatial overlapping. Co-occurrence values were taken as indicators of the fact that co-occurrent species used the same space. In this way the space was circumscribed to the micro-habitat of each trap station influential area. Only resident animals were taken into account for co-occurrence computation. Residents were defined as animals caught more than once in the same or different sampling periods.

Between 1992 and 1994, traps were fitted with a timer started by trap closing to determine activity times of animals in the field. The time elapsed between capture and trap checking was recorded. In this way each animal capture time could be estimated. Activity time was taken as a measure of animal activity periods in the grid area. A total of 511 capture times were registered, 362 of *A. azarae* and 149 of *C. venustus*.

Trapped animals were weighed, measured and marked with a numerical code in the ears. Sex and reproductive state (males: scrotal or abdominal testicles, females: perforated or imperforated vagina, nipples visible or not) were also recorded.

Data were analysed by considering separately the non-reproductive period (May to August) and the reproductive period (September to April) since it was found that spatial use and activity times are likely to vary according to the seasons or to the annual cycle of the population (O'Farrel 1974; Muñoz-Pedreros et al. 1990; Frank and Heske 1992; Muñoz-Pedreros 1992).

Population size was estimated by computing the minimum number of animals known alive (MNKA) (Krebs 1966).

Co-occurrence between *A. azarae* and *C. venustus* was analysed by means of Cole (1949) association index: $C = a \cdot d - b \cdot c/(a + b) \cdot (b + c)$ if $a \cdot d \geq b \cdot c$; or $C = a \cdot d - b \cdot c/(a + b) \cdot (a + c)$ if $b \cdot c > a \cdot d$ and $d \geq a$; or $C = a \cdot d - b \cdot c/(b + d) \cdot (c + d)$ if $b \cdot c > a \cdot d$ and $a > d$; and co-occurrence percentage $(a \cdot 100/a + e)$; where a = number of trapping stations where both species were captured, b = number of trapping stations where only the first species was captured, c = number of trapping stations where only the second species was captured, d = number of trapping stations where none of the species was captured and e = number of trapping stations where the less frequent species was captured.

The relationship between population sizes of the species and between population sizes and monthly co-occurrence was established by means of Lineal Regression Analysis, in which co-occurrence was considered as the dependent variable and population size of each species as the independent variable.

Temporal variation between *A. azarae* and *C. venustus* was determined by the Chi-square test of independence.

Results and discussion

From April 1990 throughout February 1995, 510 *A. azarae* (1,374 captures), 300 *C. venustus* (529 captures) were trapped during 14,880 trap-nights. Figure 1 shows the variations in abundance mean values after 5 sampling years for *A. azarae* and *C. venustus*. *A. azarae*

was the most abundant species for the major part of the two periods in each sampling year, the abundance values being at their minimum in spring and at their maximum in autumn-winter. The displacement in population peaks between the species under study is noticeable. The abundance, throughout the 57 months of census, of *A. azarae* did not vary significantly in relation to the abundance of *C. venustus* ($R^2 = 0.031$; D.F.: 55). This fact suggests that interference competition is not involved. As studies by Geuse and Bauchau (1985) show for *Clethrionomys glareolus* and *Apodemus sylvaticus*, we can also assume that the absence of relation between presence or abundance of one species and the other is evidence of a low interspecific competition.

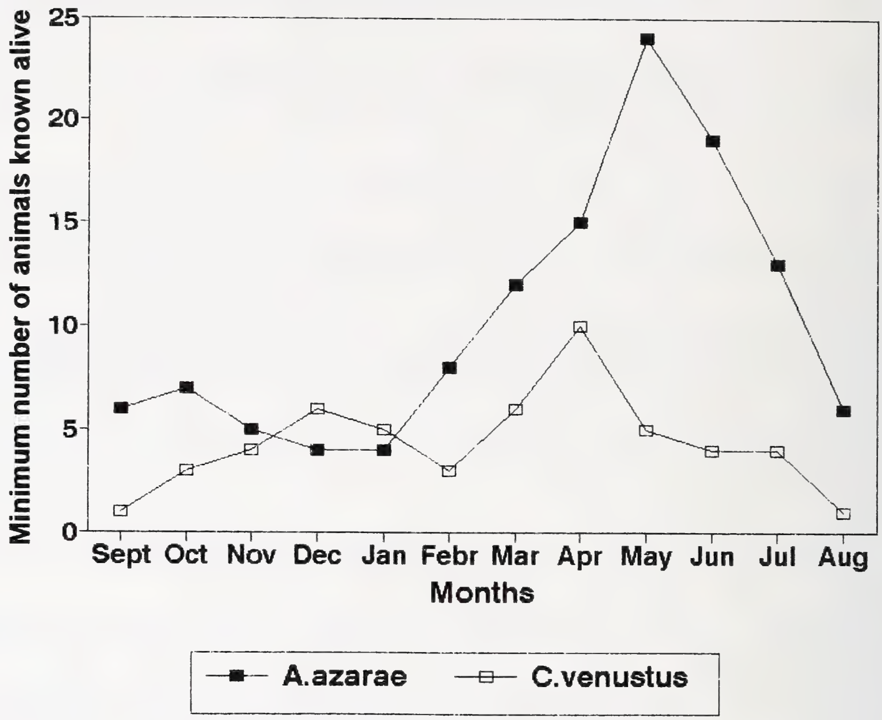


Fig. 1. Average values of monthly abundance variation (MNKA) for *Akodon azarae* and *Calomys venustus* in railway banks habitats (Río Cuarto Department, Córdoba, Argentina, 1990–1995).

Results about spatial dimension did not reveal a separation between *A. azarae* and *C. venustus* since neither species showed differences in spatial use, keeping co-occurrence in both reproductive and non-reproductive periods. The values of the Cole association index and co-occurrence percentages for non-reproductive and reproductive periods are shown in table 1. Differences in spatial use were detected and a higher co-occurrence was observed in the non-reproductive period. The high co-occurrence values (values >20%) between *A. azarae* and *C. venustus* were associated to low and positive values of the Cole association index, and related to a random spatial use. Individuals from both species co-occurred in a trap station with members of the opposite as well as the same sex. Co-occurrent animals included both young and adult individuals. Given the possibility of higher co-occurrence frequency in the non-reproductive period due to more abundance, determination of differences in co-occurrence degree between sampling periods became of paramount importance. In this way it was possible to verify whether differences in co-

occurrence represented differences in social spacing or just density differences. When determining the ratio of co-occurrence proportion over population sizes the values were: 0.12 (D.F.: 48) and 0.25 (D.F.: 48) for *A. azarae* and *C. venustus*, respectively. These results show that the two species are not likely to be conditioned by a social factor in space use, i. e., individuals from both species would not feel compelled to co-occur because of abundance. Instead, they would co-occur due to absence of territoriality among them. Brown and Orians (1970) observed that absence of interspecific territoriality is economically beneficial in habitats where high restriction in exploitation models prevents adequate divergence in resource use. This is the railway banks case, i. e. heterogeneous habitats compared to the rest of agroecosystem habitats, but they do not offer a large variety of microhabitats which allow a differential resource exploitation.

Table 1. Cole association index and co-occurrence percentage by annual period in *A. azarae* and *C. venustus* of resident populations in railway banks (Córdoba, Argentina).

	Non-reproductive period		Reproductive period	
	A. azarae n = 368	*C. venustus* n = 84	*A. azarae* n = 356	*C. venustus* n = 168
Co-ocurrence %	35.7		20.2	
Cole index	0.05		0.02	

n = number of individuals on which Cole index and co-occurrence percentages were estimated.

An important separation between *A. azarae* and *C. venustus* was observed in the niche temporal axis for reproductive and non-reproductive periods. Thus, *A. azarae* showed 24-hour activity with peaks varying according to the population annual cycle, whereas activity of *C. venustus* concentrated in crepuscular and night hours (Figs. 2 and 3). A similar behaviour to that of *A. azarae* was previously observed in other species of *Akodon* (Muñoz-Pedreros et al. 1990). In the reproductive period *A. azarae* activity decreased during daytime shifting to evening and night. In the same period *C. venustus* increased its activity times between evening and dawn with peaks between 9.00 p. m. and 3.00 a. m. (Fig. 2). In the reproductive period the differences among activity times in both species were statistically significant (Chi-square = 66.08; $P = 9.10 \times 10^{-12}$; D. F.: 7). During the non-reproductive period, differences in activity times between *A. azarae* and *C. venustus* were statistically significant with a Chi-square value of 65.77 ($P = 1.05 \times 10^{-7}$; D. F.: 7). *A. azarae* was active mainly during daytime and crepuscular hours, increasing its activity between 6.00 a. m and 9.00 p. m., whereas *C. venustus* was particularly active between 6.00 p. m. and midnight (Fig. 3). Although activity time differences were significant in both periods, higher temporal segregation took place in the non-reproductive period in which *A. azarae* showed a more diurnal behaviour. This could be accounted for by a more pronounced co-occurrence in the spatial axis during this period. However, a comparison between co-occurrence values in capture stations and population sizes of each species showed they were not conditioned by a social factor in space use. Nonetheless, differential time use in the same space could be a hiding factor. Differences in activity times due to the need of reducing the possibility of encounters, have been reported for other rodent species (Lambin and Bauchau 1989). Evidence about *A. azarae* and *C. venustus* diet (Bilenca et al. 1992; Polop 1996) shows partial overlapping. Consequently, a higher differentiation in the activity times may be the main mechanism for the use of the same space and food. This conclusion agrees with that of Carothers and Jaksic (1984) who hold that differences in activity times are generated by interference competence, as a way to make coexistence

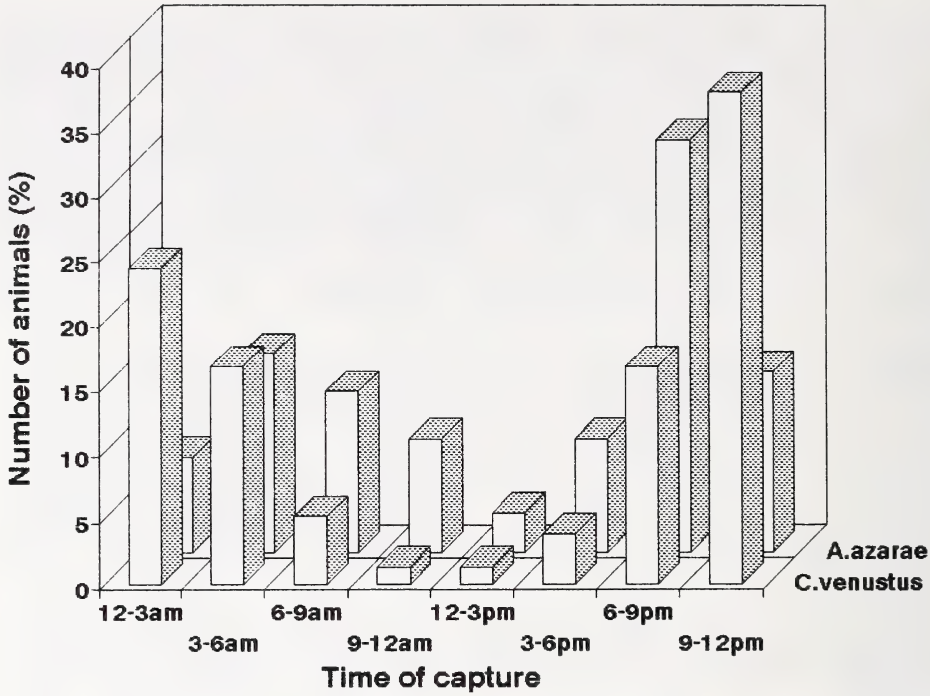


Fig. 2. Temporal distribution of *Akodon azarae* and *Calomys venustus* during the reproductive period in railway banks (Río Cuarto Department, Córdoba, Argentina).

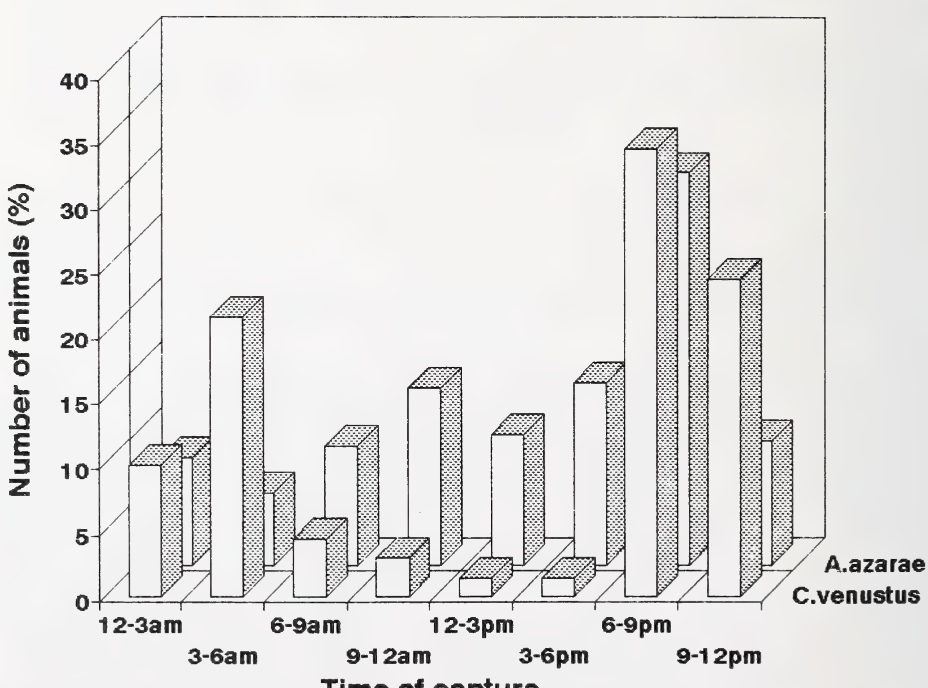


Fig. 3. Temporal distribution of *Akodon azarae* and *Calomys venustus* during the non-reproductive period in railway banks (Río Cuarto Department, Córdoba, Argentina)

feasible among species presenting agonistic interaction. Anyway, it is commonly held that only experimental data reveal interference competence (SCHOENER 1983). Also, segregation in niche dimensions in sympatric populations may reflect either the effects of past or present competition or the ecological preferences of allopatric ancestors that coexist today (CONELL 1980). Although there are no data available about the evolutionary past of these species, we know that they come from regions and probably from habitats completely different from the sampled ones (REIG 1986) and that they are morphologically and physiologically well adapted to habitats like the one under study (KRAVETZ and POLOP 1983; ZULETA 1989). Sympatric coexistence among these species might therefore be explained in the same way as that suggested by CANOVA (1993) for *Apodemus sylvaticus* and *Clethrionomys glareolus* because *A. azarae* and *C. venustus* originally lived in different habitats. Segregation in the present niche dimensions might, therefore, reflect the habitat, food preferences and activity times imposed by their original habitats.

Acknowledgements

We thank Mr. MARCOS TORRES for his work in the field and Dr. OLIVER PEARSON for the critical revision of the manuscript.

Zusammenfassung

Nutzung von Raum und Zeit bei syntopischen Populationen von Akodon azarae und Calomys venustus (Rodentia, Muridae).

Gegenstand der Studie waren die Nutzung des Raums und die aktiven Zeiten bei syntopischen Populationen von *Akodon azarae* und *Calomys venustus* in Agro-Ökosystemen im Süden der Provincia de Córdoba (Argentina). Die Raumnutzung wurde mittels des Registers des gleichzeitigen Auftretens der beiden Arten in derselben Fallenanlage bestimmt, während die aktiven Zeiträume mittels mit Chronometern ausgestatteten Fallen erhalten wurden, die sich im Moment der Gefangennahme aktivierten. Die Daten wurden je nach reproduktiver und nicht-reproduktiver Periode analysiert. Dabei wurde das gleichzeitige räumliche Auftreten von *A. azarae* und *C. venustus* sowohl während der reproduktiven als auch während der nicht-reproduktiven Periode festgestellt. Auf der zeitlichen Achse des Ökosystems konnte jedoch eine Trennung der beiden untersuchten Arten beobachtet werden. *A. azarae* zeigte eine kontinuierliche Aktivität mit je nach der reproduktiven oder der nicht-reproduktiven Periode variierenden Spitzenwerten, während *C. venustus* in beiden Perioden vor allem in Stunden der Abenddämmerung und der Nacht aktiv war. Diese Unterschiede in den Nutzungszeiten der Ressourcen konstituieren daher den Mechanismus der Koexistenz bei Syntopie von *A. azarae* und *C. venustus.*

References

BILENCA, D. N.; KRAVETZ, F. O.; ZULETA, G. A. (1992): Food habits of *Akodon azarae* and *Calomys laucha* (Cricetidae, Rodentia) in agroecosystems of central Argentina. Mammalia **56**, 372–383.

BROWN, J. M.; ORIANS, G. H. (1970): Spacing patterns in mobile animals. Ann. Rev. Ecol. Syst. **1**, 239–262.

CABRERA, A. (1953): Esquema fitogeográfico de la República Argentina. Revista Museo de la Plata, Botánica **8**, 87–168.

CANOVA, L. (1993): Resource partitioning between the bank vole *Clethrionomys glareolus* and the wood mouse *Apodemus sylvaticus* in woodland habitats. Boll. Zool. **60**, 193–198.

CAROTHERS, J. H.; JAKSIC, F. M. (1984): Time as the niche difference: the role of interference competition. Oikos **42**, 403–406.

COLE, L. C. (1949): The measurement of interespecific association. Ecology **30**, 411–424.

CONELL, H. J. (1980): Diversity and the coevolution of competition, or the ghost f competition past. Oikos **35**, 131–138.

Crespo, J. A. (1966): Ecología de una comunidad de roedores silvestres en el Partido de Rojas, Provincia de Buenos Aires. Rev. Mus. argent. Cienc. nat. "Bernardino Rivadavia" Inst. nac. Invest. Cienc. nat. (Ecol.) **1**, 79–134.

Dalby, P. L. (1975): Biology of pampa rodents, Balcarce Area, Argentina. Publs Mus. Mich. St. Univ. Biol. Ser. **5**, 149–271.

Frank, D. H.; Heske, E. J. (1992): Seasonal changes in space use patterns in the southern grasshopper mouse, *Onychomys torridus torridus*. J. Mammalogy **72**, 293–298.

Geuse, P.; Bauchau, V. (1985): *Apodemus sylvaticus* et *Clethrionomys glareolus*: competition or coexistence?. Annls. Soc. R. Zool. Belg. **2**, 221–230.

Hutchinson, G. E. (1957): Concluding remarks. Cold Spring Harbor Symposium on Quantitative Biology **22**, 415–427.

Kravetz, F. O.; Polop, J. J. (1983): Comunidades de roedores en agroecosistemas del Departamento Río Cuarto, Córdoba. Ecosur **10**, 1–18.

Krebs, C. J. (1966): Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. **36**, 239–273.

Lambin, X.; Bauchau, V. (1989): Contest competition between wood mouse and bank vole: is there a winner? Acta Theriol. **34**, 385–390.

Meserve, P. L. (1981): La utilización de recursos en roedores simpátricos; el papel del hábitat. Medio Ambiente **5**, 96–114.

Muñoz-Pedreros, A. (1992): Ecologia del ensamble de micromamíferos en un agroecosistema forestal de Chile central. Hist. Nat. (Chile) **65**, 417–428.

Muñoz-Pedreros, A.; Murua, R; Gonzales, L. (1990): Nicho ecológico de micromamíferos en un agroecosistema forestal de Chile central. Hist. Nat. (Chile) **63**, 267–277.

O'Farrell, M. J. (1974): Seasonal activity patterns of rodents in a sagebrush community. J. Mammalogy **55**, 809–823.

Pearson, O. P. (1967): La estructura por edades y la dinámica reproductiva en una población de ratones de campo, *Akodon azarae*. Physis **27**, 53–58.

Polop, J. J. (1996): Análisis de las respuesta adaptativa del género *Calomys*. Ph. D. thesis, Universidad Nacional de Río Cuarto, Río Cuarto, Argentina.

Polop, J. J.; Sabattini, S. (1993): Rodent abundance and distribution in habitats of agrocenosis in Argentina. Studies on Neotropical Fauna and Environment **28**, 39–46.

Polop, J. J.; Martinez, R. L.; Torres, M. P. (1985): Distribución y abundancia de poblaciones de pequeños roedores en la zona del Embalse de Río Tercero, Córdoba. Hist. Nat. (Argentina) **5**, 33–44.

Reig, O. (1986): Diversity patterns and differentiation of High Andean Rodents. In: High altitude tropical biogeography, Ed. by F. Vuilleumier and M. Monasterio. New York: Oxford University Press. Pp. 404–439.

Schoener, T. W. (1974): Resource partitioning ecological communities. Science **185**, 27–39.

Schoener, T. W. (1983): Field experiments on interespecific competition. Am. Nat. **122**, 240–285.

Zuleta, G. A. (1989): Estrategias de historia de vida en el ratón del pastizal pampeano, *Akodon azarae*. PhD thesis, Buenos Aires University.

Authors' address: José W. Priotto and Jaime J. Polop, Departamento de Ciencias Naturales, Facultad de Ciencias Exactas, Físico-Químicas y Naturales, Universidad Nacional de Río Cuarto, Agancia Postal N° 3, 5800, Río Cuarto, Córdoba, Argentina.

Z. Säugetierkunde **62** (1997) 37–42

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Cytogenetics of Silky desert mice, *Eligmodontia* spp. (Rodentia, Sigmodontinae) in central Argentina

By S. I. Tiranti

Department of Biological Sciences, Texas Tech University, Lubbock, Texas, USA

Receipt of Ms. 29. 03. 1996
Acceptance of Ms. 03. 06. 1996

Abstract

Chromosomal features of *Eligmodontia typus* and *E. morgani* are described for six localities from central Argentina to better understand their geographic distribution. A chromosomic study of *Eligmodontia* revealed the finding of a $2n = 34$ karyotype, previously described as an intrapopulation polymorphism, in 15 specimens from Laguna Blanca National Park, Neuquén. Information regarding the distribution of the $2n = 44$ karyotype corresponding to *E. typus* in four localities of La Pampa and one of eastern Neuquén, Argentina is provided.

Introduction

Chromosomes have been shown to be a valuable means for the identification of specific status in many animal species. Through cytogenetic studies synmorphic taxa that for long had been considered single species, have been found to represent more than one taxon (Baker 1984). The genus *Eligmodontia* Cuvier, 1837, whose species are known as highland desert or silky desert mice, has been considered monotypic (Hershkovitz 1962; Nowak and Paradiso 1983), despite the fact that up to seven putative species have been described (Ortells et al. 1989). Recently, the number of species recognized in the genus has ranged from three species which were based on karyological confirmation (Steppan 1995; *morgani* Allen, 1901, *puerulus* Philippi, 1896, and *typus* Cuvier, 1837) to six species where morphology was used as the primary taxonomic feature (Braun 1993; *hirtipes*, Thomas, 1902; *marica* Thomas, 1918, *moreni* Thomas, 1986, *morgani*, *puerulus*, and *typus*). In central and southern Argentina this genus is composed of two chromosomally distinct cytotypes (Ortells et al. 1989; Kelt et al. 1991; Zambelli et al. 1992), which are *Eligmodontia typus* with a diploid number of 43–44 chromosomes, and *E. morgani* with $2n = 32$–33. Prior to these findings, generally all *Eligmodontia* in this area were referred to as *E. typus* (e.g. Pearson et al. 1987), following the unifying criteria of Cabrera (1961) and Hershkovitz (1962); but lately, Patagonian *Eligmodontia* have been recognized in ecological studies as *E. morgani* (Pearson 1994; Saba and Lamo 1994). Recognizing that both taxa appear to be synmorphic and with a wide distribution, it would be necessary to assertain their karyology in order to be able to assign systematic identification. Nevertheless a word of caution on the use of "chromosomal formulae as a diagnostic key to species identifications" was forwarded by Musser and Carleton (1993) on the grounds of "the complex interdigitation of specific ranges among the ridges and valleys of the southern Andes" and the need of a revision of the genus. In addition, the other species of *Eligmodontia* for which chromosomal informa-

tion is available are *E. puerulus* with 2 n = 50, inhabiting southern Peru and western Bolivia (Ortells et al. 1989; Kelt et al. 1991) and *E. moreni* from northern Argentina with 2 n = 34 (Spotorno et al. 1994).

Material and methods

A total of 27 *Eligmodontia* specimens were live-trapped with Sherman, Davis and wire mesh traps. The standard procedure of in-vivo colchicine mitotic arrest was used for obtaining chromosomes from bone marrow. In most cases the yeast stress method (Lee and Elder 1980) was used to obtain a higher mitotic index. Slides were produced by dropping the cell suspension from a 50–60 cm height into a large drop of distilled water on the surface of the slide (Baker et al. 1982). Chromosome slides were observed and photographed and the diploid number and chromosomal morphology was determined for each specimen from photographs. Voucher specimens were prepared as standard study skins and skulls and are housed in the collections of Texas Tech University Museum (TTU), and the collection of Universidad Nacional de Rio Cuarto (UNRC).

Localities sampled (Fig. 1) and specimens studied: TK numbers identify slides and cell suspensions from voucher specimens.

Eligmodontia morgani

Neuquén: Zapala department: Laguna Blanca National Park (n = 15). TK 40 245 male, TK 40 248 female, TK 40 266 female, TK 40 287 male, TK 40 291 female, TK 40 292 male, TK 40 293 male, TK 40 294 female, TK 40 295 female, TK 40 298 female, TK 40 299 female, TK 40 300 male, TK 47 601 male, TK 47 602 male, TK 47 603 female.

Eligmodontia typus

Neuquén: Zapala department, 20 km E Zapala (n = 1). TK 40 239 male. La Pampa: Toay department: Estancia Los Toros, 12 km NNE Naicó (n = 7). TK 27 886 male, TK 27 887 female, TK 27 890 male, TK 40 618 male, TK 40 623 male, TK 40 624 female, TK 40 629 male. Lihué Calel department, Puesto Las Lagunitas, 60 km SE Puelches (n = 1). TK 47 610 female. Puelén department, 25 km SE Puelén (n = 2). TK 47 612 female, TK 47 613 male. Cerro Colón (n = 1). TK 47 623 female.

Results and discussion

The geographic distribution of cytotypes is shown in figure 1 and the karyotypes of *Eligmodontia typus* and *E. morgani* are shown in figures 2 and 3 respectively.

Regarding *Eligmodontia typus*, the common usage has been to take for granted that the 2 n = 44 karyotype belongs to this species, existing also a 2 n = 43 variant (Ortells et al. 1989; Kelt et al. 1991; Zambelli et al. 1992). The 2 n = 44 karyotype described originally from Laguna Chasicó, Buenos Aires province (Ortells et al. 1989), seems to show little variation and is widespread throughout its range. It consists of a pair of large metacentric autosomes, 20 pairs of acrocentrics, and being the X chromosome a metacentric and the Y a subtelocentric (Fig. 2). This karyotype was found from a total of 12 specimens from all La Pampa and E Neuquén localities in which the 2 n = 43 variant was not detected.

At Laguna Blanca National Park a 2 n = 34 karyotype consisting of 16 pairs of acrocentric autosomic chromosomes, with the X chromosome telocentric and Y chromosome metacentric, was found in all 15 specimens studied (Fig. 3). Originally this karyotype was described by Zambelli et al. (1992) for *Eligmodontia* sp. from one locality in Neuquén province, and one locality in Rio Negro province. This results in a northward extension of about 120 km for this karyotype.

Fig. 1. Neuquén and La Pampa provinces, central Argentina with collecting localities: 1. Laguna Blanca National Park. 2. 20 km E Zapala. 3. 25 km SE Puelén. 4. Cerro Colón. 5. Puesto Las Lagunitas. 6. Estancia Los Toros. Asterisks denote the 2 n = 44 karyotype and the solid circle the 2 n = 34.

Previously, Ortells et al. (1989) had described 2 n = 32–33 karyotypes for specimens of *Eligmodontia* sp. The 2 n = 32 karyotype consisted of 14 pairs of acrocentric autosomes and a pair of small metacentrics. A polymorphism involving an heteromorphic pair composed of one small metacentric and two small acrocentrics produced the 2 n = 33 variant. For both karyotypes the X was telocentric and Y metacentric. Later, Kelt et al. (1991) described further 2 n = 32 karyotypes from other Patagonian localities and gave reasons for the assignment of these forms to *E. morgani.* Furthermore, the 32, 33 and 34 variants were demonstrated, though G-banding and meiotic studies to "belong to one polymorphic system involving a Robertsonian fusion" (Zambelli et al. 1992).

What is unusual is the fact that all the specimens studied from the Laguna Blanca population possess the 2 n = 34 karyotype, indicating that this chromosomal variant is fixed or that a more extensive distribution of all 2 n = 34 populations remains to be discovered.

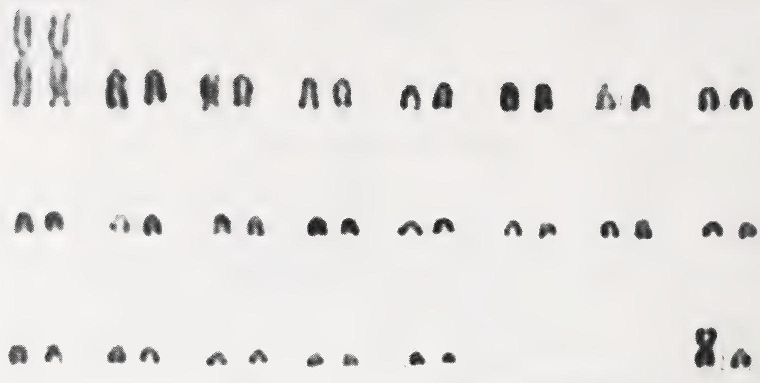


Fig. 2. *Eligmodontia typus* 2 n = 44 karyotype from 25 km SE Puelén, La Pampa (TK 47 613 male).

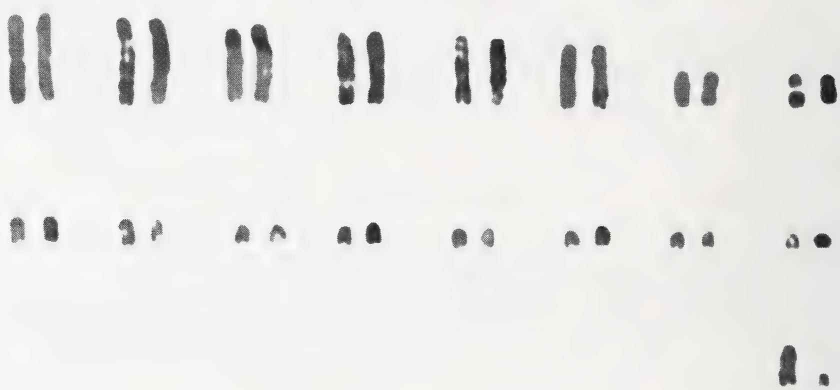


Fig. 3. *Eligmodontia morgani* 2 n = 34 karyotype from Laguna Blanca National Park, Neuquén. (TK 47 602 male).

Zambelli et al. (1992) found the 2 n = 32–33 and 2 n = 44 cytotypes, of *Eligmodontia* sp. and *E. typus* respectively, in sympatry in two localities of Neuquén and Rio Negro provinces. Unfortunately, detailed habitat data to support habitat segregation of the two species has not been described.

In this report both *Eligmodontia* karyotypes (2 n = 34 and 2 n = 44) were found ca. 50 km apart in Neuquén province. The site in which the 2 n = 34 karyotype was found is located in a typical Patagonian shrub-steppe habitat with *Mulinum spinosum* being one of the dominant shrubs. Alternatively, the 2 n = 44 *E. typus* (a single specimen) locality 20 km E Zapala is found in the Monte Desert shrublands, comprised mostly of creosote bush (*Larrea divaricata*) and molle (*Schinus* sp.). How exactly the two cytotypes are distributed in specific habitats is yet to be documented. Mares et al. (1981) did find the morphological types to be habitat specific and this is comparable to the hypothesis that the distribution of cytotypes will reflect the habitat distribution.

It has been argued (Musser and Carleton 1993) of the possibility that the assignment of the 2n = 32–33 karyotype to *E. morgani* by Kelt et al. (1991) could be doubtful, considering that the specimens studied by these authors did not come from the type locality, but from 70 km away. These same karyotypes described by Ortells et al. (1989) were not assigned by these authors to any particular species and neither the 2n = 34 variant discovered by Zambelli et al. (1992). We suggest that the opinion of Kelt et al. (1991) in the use of the name *morgani* for these polymorphic complex of 2n = 32 to 34 should be followed until further research finally resolves this problem.

Acknowledgements

The author's work in La Pampa province was supported by the Subsecretaría de Cultura, where N. Durango, G. Siegenthaler, and E. Fiorucci contributed in many ways to the accomplishment of this report. Stay at Texas Tech University is supported in part by the Dirección Nacional de Cooperación Internacional, Ministerio de Cultura y Educación, Argentina and the Universidad Nacional de La Pampa, Argentina. Localities Cerro Colón, 25 km SE Puelén and Puesto Las Lagunitas were sampled as part of La Pampa Province Vertebrate Survey. R. J. Baker critically reviewed and provided many helpful suggestions on the first drafts of the manuscript.

Zusammenfassung

Cytogenetik von Seidenwüstenmäusen, Eligmodontia spp. (Rodentia, Sigmodontinae) in Mittelargentinien

Um zum Verständnis ihrer Verbreitung und Biogeographie beizutragen, werden chromosomale Merkmale von Arten der Gattung *Eligmodontia* aus Mittelargentinien beschrieben. Insbesondere werden chromosomale Besonderheiten von *Eligmodontia typus* und *E. morgani* aus sechs Gebieten in Mittelargentinien vorgestellt. Bei 15 Individuen aus dem Laguna Blanca Nationalpark, Neuquén, wurde ausschließlich der Karyotyp 2n = 34 gefunden. Dieser Karyotyp war von anderen Autoren als Element eines Chromosomenpolymorphismus bei *Eligmodontia* beschrieben worden. Die Verbreitung des für die Art *E. typus* charakteristischen Karyotyps 2n = 44 wird für vier Gebiete von La Pampa und ein Gebiet aus dem östlichen Neuquén dargestellt.

Literature

Baker, R. J. (1984): A sympatric cryptic species of mammal: A new species of *Rhogeessa* (Chiroptera: Vespertilionidae). Syst. Zool. **33**, 178–183.

Baker, R. J.; Haiduk, M. W.; Robbins, L. W.; Cadena, A.; Koop, B. F. (1982): Chromosomal studies of South American bats and their systematic implications. In: Mammalian biology in South America. Ed. by M. A. Mares and H. H. Genoways. Spec. Publ. Ser., Pymatuning Lab. Ecol., Univ. Pittsburgh **6**, 303–327.

Braun, J. K. (1993): Systematic relationships of the tribe Phyllotini (Muridae: Sigmodontinae) of South America. Spec. Publ. Norman: Oklahoma Museum of Natural History. Pp. 1–50.

Cabrera, A. (1961): Catálogo de los mamíferos de America del Sur. Revista del Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" **4**, 309–732.

Hershkovitz, P. (1962): Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zool. **46**, 1–524.

Kelt, D. A.; Palma, R. E.; Gallardo, M. H.; Cook, J. A. (1991): Chromosomal multiformity in *Eligmodontia* (Muridae, Sigmodontinae), and verification of the status of *E. morgani*. Z. Säugetierkunde **56**, 352–358.

Lee, M. R.; Elder, F. F. (1980): Yeast stimulation of bone marrow mitoses for cytogenetic investigation. Cytogenet. Cell Genet. **26**, 36–40.

Mares, M. A.; Ojeda, R. A.; Kosko, M. P. (1981): Observations on the distribution and ecology of the mammals of Salta Province, Argentina. Annals Carnegie Museum **50**, 151–206.

Musser, G. G.; Carleton, M. D. (1993): Family Muridae. In: Mammal Species of the World. A taxonomic and geographic reference. Ed. by D. E. Wilson and D. A. M. Reeder. 2. ed. Washington and London: Smithsonian Institution Press. Pp. 501–755.

Nowak, R. M.; Paradiso, J. L. (1983): Walker's Mammals of the World. Fourth edition. Vol. 2. Baltimore and London: John Hopkins University Press. Pp. 569–1362.

Ortells, M. O.; Reig, O. A.; Wainberg, R. L.; Hurtado de Catalfo, G. E.; Gentile de Fronza, T. M. L. (1989): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae). II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*. Z. Säugetierkunde **54**, 129–140.

Pearson, O. P. (1994): The impact of an eruption of Volcán Hudson on small mammals in Argentine Patagonia. Mastozoología Neotropical **1**, 103–112.

Pearson, O.; Martin, S; Bellati, J. (1987): Demography and reproduction of the silky desert mouse (*Eligmodontia*) in central Argentina. Fieldiana Zoology New Ser. **39**, 433–446.

Saba, S. L.; Lamo, D. A. de (1994): Dynamic responses of mammals to the eruption of Volcán Hudson. Mastozoología Neotropical **1**, 113–122.

Spotorno, A. E.; Sufan-Catalan, J.; Walker, L. I. (1994): Cytogenetic diversity and evolution of Andean species of *Eligmodontia* (Rodentia, Muridae). Z. Säugetierkunde **59**, 299–308.

Steppan, S. J. (1995): Revision of the tribe Phyllotini (Rodentia: Sigmodontinae), with a phylogenetic hypothesis for the Sigmodontinae. Fieldiana Zool. New Ser. **80**, 1–112.

Zambelli, A.; Dyzenchauz, F.; Ramos, A.; Rosa, N. de; Wainberg, R.; Reig, O. A. (1992): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae). III. New data on the distribution and variability of karyomorphs of the genus *Eligmodontia*. Z. Säugetierkunde **57**, 155–162.

Author's address: Sergio I. Tiranti: Department of Biological Sciences, Texas Tech University, Lubbock, Texas 79409-3131, USA.

Z. Säugetierkunde **62** (1997) 43–52

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The ecology and natural history of a fishing mouse *Chibchanomys* spec. nov. (Ichthyomyini: Muridae) from the Andes of southern Ecuador

By A. A. Barnett

Fauna and Flora International, Cambridge UK

Receipt of Ms. 29. 12. 1995
Acceptance of Ms. 26. 03. 1996

Abstract

Information is presented on the habitat, diet, biogeography and conservation requirements of a species of *Chibchanomys* from the Andes of southern Ecuador. Naturally rare, it is a paramo stream-living species which is probably primarily a predator on aquatic macroinvertebrates, supplemented with fish. The eyes are reduced, the vibrissum and its nerves highly developed. Observations on a captive individual suggest touch has supplanted vision in food location in this species. Occuring at 4 000 m, this *Chibchanomys* is one of the highest-living members of its family. Along it a number of other vertebrates, invertebrates and plants, this rodent is restricted to the Cajas Plateau. Threats to the survival of it and the other endemic biota of the plateau are outlined.

Introduction

The Ichthyomyini is a small tribe of sigmodontine rodents (Wilson and Reeder 1993) specialized for a semi-aquatic carnivorous existence in small bodies of running water. Ichthyomyids are exclusively Neotropical, ranging from 16 23′N (northern Mexico) to 11 03′S (central Peru). Though some species occur in lowland forests, most live at high altitudes, often close to or above the tree-line. In his monograph on the systematics and ecology of the tribe, Voss (1988) lists 14 species of ichthyomyid in five genera. Since then Ochoa and Soriano (1991) have described a new species of *Neusticomys* (*N. mussoi*) from the Andes of Venezuela.

In 1981 two ichthyomyines were trapped in a small stream on the Cajas Plateau, Azuay Province, Ecuador. This was followed by another specimen in 1983 and by several live specimens in subsequent years. Three voucher specimens were deposited in the collections of The Natural History Museum, London, England. Originally the specimens were thought to belong to another ichthyomyine, *Anotomys leander* Thomas, 1906. However, closer examination has revealed them to be a new species of the genus *Chibchanomys*, erected by Voss (1988). The species is being described elsewhere. Here I present data on the ecology and natural history of this animal. It is the second known member of this genus and the sixth ichthyomyine species to be recorded for Ecuador.

Material and methods

As part of a series of zoological surveys of the Cajas Plateau, ichthyomyines were purposefully trapped for between 1981 and 1987. Trapping techniques incorporated methods and suggestions from previous

workers on these mammals (Tate 1931; Stirton 1944; Hooper 1968; Starrett and Fisler 1970; Musser and Gardner 1974). At all sites the bait was a mixture of oats, peanut butter and fresh trout flesh (sometimes substituted by tinned tuna or sardine). Traps were checked at dawn and dusk, fresh bait was provided at these times. For details of trapping effort see table 1.

Table 1. Trapping effort for *Chibchanomys* in Cajas
Combined figures for years given. Trapping at all sites occurred between July and September.

Site	No. Trap Nights	No. *Chibchanomys*	No. other animals	Trap Success (%)
Rio Mazan 2 700 m: 1986, '87	480	0	17	3.5
Zorracucho valley (Lake Llaviuco) 3 100 m: 1981, '83	200	1	20	10.0
Chirimanchi 3 300 m: 1983	50		23	46.0
Luspa 3 700 m: 1981, '83, '84	346	2	66	19.1
Torreadora 4 000 m: 1981, '83, '84	369	2	75	20.3
Athiovacu 3 900 m: 1984	121	0	22	18.2
Chapiurcu 3 750 m: 1983	100	0	32	32.0
Pogson and Lees (various sites)	700	1	525	75.0

The Cajas Plateau is the northern-most part of the Serra Machangara, an outlier of the Occidental (western) Cordillera of the Ecuadorian Andes. Rising to 4 138 m at its highest point (Mt. Soldados), it has high-altitude moorland vegetation (paramo) above about 3 100 m, and montane forest below this. The paramo vegetation of Cajas is outlined by Barnett (1992) and described in detail by Ramsay (1992). Barnett (1991) outlines the region's montane forest vegetation.

Results and discussion

Trapping and habitat

The first two specimens of *Chibchanomys* sp. nov. were taken on the same day (22 August) in 1981 from near Lake Luspa (0 2 50 S, 79 30 W: 3 700 m), in large all-metal snap traps placed at climb-out sites on the gravel-and-mud banks of a small bush-covered island in the middle of a small, clear, cold, fast flowing stream, downstream from a small (2.5 m) waterfall. The water was no more than 40 cm deep at any point and appeared extremely well-oxygenated. The bottom was of coarse gravel, stones and bedrock interspersed with large boulders. The stream averaged 1 m wide over most of its length, and ran through an area dominated by tussocks of *Calamagrostris* bunch grass, with scattered shrubs including *Hypericum* (Hypericaceae) and *Bacharis* (Asteraceae). With the exception of algal films on rocks, there was no obvious aquatic vegetation.

Repeat trapping at this locality in 1983 and 1984 yielded no further specimens. In August 1983 in a similar, though slightly more sheltered, habitat near Lake Torreadora (0 2 48 S, 79 17 W: 4 000 m) two *Chibchanomys* sp. nov. were caught alive in Longworth live traps, positioned near water on small stone and mud beaches. One trap was set adjacent

to the water, with guide sticks to the water's edge to funnel in rodents (see Barnett and Dutton 1995). The other was placed in a prominent run at the junction of a beach and the base of an overhang in the bank and faced a hole in the bank, just downstream from a small waterfall. To avoid loss, live-traps were securely tied and weighted with rocks on top of the box. Both animals came from the same (unnamed) stream, which had also been trapped in 1981. In 1983, neighbouring streams of similar appearance were also trapped, but none yielded specimens. The Torreadora animals were kept for observation, but unfortunately escaped before any studies could be made.

Trapping in the Zorracucho valley, on a stream entering the glacial moraine-empounded Lake Llaviuco (0 2 51 S, 79 0 1 W: 3 100 m), yielded one *Chibchanomys* sp. nov. on 7 August 1983. This watercourse was unlike the others from which specimens had been taken. It was between 1.5 and 3 m wide and, in places, the depth exceeded 2 m. The water was sometimes quite muddy and the bottom was a mixture of large (more than 25 cm diameter) stones and mud. The stream was surrounded by land grazed by cows at low intensity. The animal was taken by one of several metal snap traps suspended down a near vertical mud bank to holes (roughly 10 to 25 cm in diameter) just above the water line. It is possible that the animal could have been washed down from further upstream. In July 1981 trapping in the marshland surrounding Lake Llaviuco did not find any ichthyomyines.

Three of the five specimens which I trapped were taken in proximity to small waterfalls. A number of other workers have recorded a similar predilection in other species (Hooper 1968; Starrett and Fisler 1970 for *Rheomys*; Musser and Gardner 1974 for *Neusticomys*; Voss 1988 for *Chibchanomys* and *Ichthyomys*). There are also a number of previous records of ichythomyines using small emergent objects to rest, feed and groom (see Enders 1939; Stirton 1944; Hooper 1968; Starrett and Fisler 1970, for *Rheomys*; Musser and Gardner 1974 for *Daptomys*). This may be a typical piece of ichthyomyine behaviour and could be of use in further fieldwork (see also Stirton 1944).

These habitat features have been found to be of use in surveying other stream-living small mammals (see Woodall 1993; Giraudoux et al. 1995 as examples). Jim and Teresa Clare (pers. comm. 1994) report that on 24 April 1992 their field staff, Andrea Pogson and Caroline Lees, trapped one specimen of *Chibchanomys* sp. nov. on the bank of a small (1.8 m wide) stream "flowing out of Laguna Luspa" at 3 800 m for a BBC-National Geographic wildlife film "Avenue of the Volcanoes". The animal was caught in a Longworth livetrap after an effort of 700 trap nights, extending over 5 months. The trap was positioned about 45 cm from the stream, facing the waters' edge and baited with fresh trout flesh.

Reflecting the views of Voss (1988), that ichthyomyines do not live in still water, *Chibchanomys* sp. nov. was not caught by seeps, standing pools or lakes in the paramo. This is despite considerable trapping effort being expended placing traps at suitable sites around the edges of such places between July and September 1981, 1983 and 1984 by myself and in 1991 and 1992 by Pogson and Lees (although Jim and Teresa Clare [pers. comm. 1994] report that "some people claimed to have seen them around floating vegetation at the edge of lakes"). At lower altitude, in the montane forests of the Cajas Plateau, there was no success in 200 trap nights in small, steep, fast-flowing streams of the Rio Mazan valley (0 2 53 S, 78 59 W: 2 700 m to 3 050 m), nor another 280 trap nights on the banks of the Rio Mazan itself (August 1986 and September 1987). Also unsuccessful were 50 trap nights along bush-covered banks of a stream in the transition zone between montane forest and paramo grassland (Chirimanchi, 0 2 52 S, 79 0 5 W; 3 300 m, August 1983), and on two streams in high paramo (Athiovacu, 0 2 53 S, 80 0 5 W; 3 900 m, August 1984, 121 trap nights: Chapiurcu 0 2 54 S, 80 0 5 W; 3 750 m, July 1983, 100 trap nights).

The records for *Chibchanomys* sp. nov. are between 3 100 m and 4 000 m and only in streams flowing through areas of open grassy vegetation. The streams resemble those in

which Robert Voss trapped *Anotomys leander* in northern Ecuador (see Voss 1988), and contrasts with the situation for *Chibchanomys trichotis* (Thomas, 1897), which Voss (1988) describes as "a typical Andean brook … flow(ing) over cobble and among large boulders" in montane forest. He reports that pools were present, in which organic detritus had accumulated, and that a canopy of woody plants shaded the stream. This closely resembles the montane forest habitat of Rio Mazan where I trapped, unsuccessfully, for *Chibchanomys*. It is not unusual for different members of an ichthyomyine genus to occur in separate habitats. In *Ichthyomys*, for example, species occur in paramo (*I. hydrobates* Winge, 1891), montane forest (*I. stolzmani* Thomas, 1893) and lowland forest (*I. tweedii* Anthony, 1921), and a similar situation exists in *Rheomys* (see Voss 1988).

The previous highest record for *Chibchanomys* was 2 900 m in Colombia, the records from Cajas extend the known altitude range of the genus by some 1 100 m and, with *Anotomys leander*, makes *Chibchanomys* sp. nov. the highest-living known ichthyomyine (see Voss 1988). *Chibchanomys* sp. nov. appears to be uncommon in Cajas. I spent a total of 1 666 trap nights trapping for them, catching 255 small mammals, of which only 5 were of this genus. In 700 trap nights along streamsides in Cajas, Jim and Teresa Clare's field assistants caught about 525 small mammals only one of which was a *Chibchanomys*.

Diet

When the body cavities of the Lake Luspa specimens were opened there was a strong smell of fish (an event also noted by Enders 1939 for *Rheomys raptor hartmanni* Enders, 1939). On-site examination with a handlens of the stomach contents showed the remains of fish (scales, bones with attached flesh), along with larvae of aquatic insects (including Ephemeroptera and Trichoptera). The stomach of the Llaviuco specimen was empty. Fecal matter from the specimens trapped live at Torreadora contained both small particles of bone and insect remains.

The eyes of *Chibchanomys* sp. nov. are very much reduced and recognition of food proximity appears to be entirely tactile, with both vibrissae and forepaws being used. Footage of the specimen photographed by Jim and Teresa Clare, clearly shows *Chibchanomys* sp. nov. eating a fish. At around 4 cm, the captured fish is about one-third the length of the rodent, and is eaten out of the water on the ground, with the forepaws holding and manipulating food and being used in a posture similar to that pictured in Voss (1988) for *I. pittieri*. Food handling behaviour resembles that described by Voss et al. (1982) for *Ichthyomys pittieri* Handley and Mondolfi, 1963 and by Starrett and Fisler (1970) for *Rheomys underwoodi* Thomas, 1906. The animal is seen apparently utilizing the tactile capabilities of its vibrissae when searching for food in shallow water of the stream edge.

Jim and Teresa Clare (pers. comm. 1994) kept their specimen captive for four months. It lived in an enclosure about 1.5 m × 1.5 m, "with vegetation from Cajas and an artificial stream and waterfall". During this time they gave it only small live fish, "which it would catch for itself out of a shallow pool in a reconstructed stream". Though using the artificial burrow provided, the animal also "made several tunnels in mossy vegetation in the set into which it would disappear with the fish". The Clares observed that the animal "was almost exclusively nocturnal though [it] did occasionally emerge during the day for short periods" and that "it would eat several fish a night. The mouse weighed 18 g on arrival and 27 g on its release".

Voss et al. (1982) noted that *Ichthyomys pittieri* made great use of its vibrissae while hunting for food, while Starrett and Fisler (1970) made similar observations on *Rheomys underwoodi*. Voss (1988) has noted that most ichthyomyines have a very well-developed trigeminal nerve, running through the infraorbital foramen and innervating the mystacial vibrissae and related the nerve's size to the vibrissum's putative food-finding function. The vibrissae of *Chibchanomys* sp. nov. are stiff, well-developed and form a

broad, arc-like array in a graded-size series. During field dissections the trigeminal nerve of *Chibchanomys* sp. nov. was seen to be very much enlarged compared to other rodents (e. g. *Akodon*, *Oryzomys*, *Thomasomys*), which were being dissected contemporaneously. From the great development of these nerves one may infer that *Chibchanomys* sp. nov. may also use its whiskers, like *I. pittieri* and *R. underwoodi*, to search for food.

Although some species of Ichthyomyini seem to favour freshwater crabs (Pseudothelphusidae) where these occur (Voss et al. 1982), most (including *Chibchanomys trichotis*, the new species' congener) appear to be primarily eaters of aquatic insects (Voss 1988). This has caused several authors (e. g. Starrett and Fisler 1970; Musser and Gardner 1974) to consider them trophically and behaviourally comparable to northern water shrews (*Neomys*) (see Churchfield 1985). Decapod crustaceans are generally absent from high-altitude streams (see Voss et al. 1982; Ward 1994; Winterbourne 1994), and none were observed at the paramo streams of Cajas nor in the montane forest streams of the Rio Mazan valley, though aquatic invertebrates (including insects) were well represented (Rose Ainesworth, pers. comm. 1988) and present in proportions typical of torrential streams (see Nielsen 1950; Turcotte and Harper 1982; Ormerod et al. 1994). The two types of insect larvae identified preliminarily from stomach contents of captured specimens were the commonest insect orders captured by Ainesworth, with Ephemeroptera being 32% of the catch and Trichoptera 26% (by numbers of individuals) (Rose Ainesworth pers. comm. 1988).

Though the number of *Chibchanomys* stomachs analysed (3) is too small for a definitive statement, the preliminary data indicates a degree of dietary selectivity by this rodent for remains of the area's most abundant aquatic macroinvertebrates were not found in these stomachs. These include large freshwater shrimps (Jim and Teresa Clare, pers. comm. 1994) and gammarids (which Rose Ainesworth [pers. comm. 1988], reported to be ubiquitous and present at densities of up to 170/m2 in streams in paramo and in montane forest). It should be noted that, though both Ainesworth and the Clares found the freshwater invertebrate communities of the Cajas area to be relatively species-rich, Ainesworth (pers. comm. 1988) is of the opinion that "the overall density of invertebrates is relatively low, probably because of high spate frequencies" (see Ali 1968 a, b; Suren 1994; Ward 1994). Under these circumstances, it is possible that fish represent a dietary supplement for *Chibchanomys* sp. nov., rather than a major food item and are resorted to when invertebrates are scarce. Fairley (1972) and Woollard et al. (1978) have shown that the persistence of scales and bones may lead to the overestimation of fish in the diet of aquatic carnivores. Consequently, despite the presence of some piscean remains, it is likely that *Chibchanomys* sp. nov. resembles *C. trichotis* and other ichthyomyines in being, primarily, an aquatic insectivore.

Biogeographical considerations

The current records for *Chibchanomys* sp. nov. lie within the known range of the genus, though it is the only member of the genus yet recorded for Ecuador. The only other known member of the genus *Chibchanomys*, *C. trichotis*, is known from four places: two (including the type locality) in Colombia (eastern Departamento Cundinamarca), on the Tachira Andes (Estado Tachira, Venezuela) and, far to the south, the Cordillera Carpish (Departamento Huanuco, Peru) (Fig. 1).

The geographic location of *Chibchanomys* sp. nov. in the middle of the apparent range of *C. trichotis* suggests that it may be appropriate to reconsider the taxonomic position of the southern, Peruvian, populations of *C. trichotis*. Voss (1988) notes that "character differences may indicate that southern populations of *Chibchanomys* [*trichotis*] are phenotypically distinctive" from those in Colombia and Venezuela, but notes that "more material is required to substantiate this conjecture", there being, at present, insufficient material to

Fig. 1. Distribution of collection localities for *Chibchanomys* (locations and grid references for *C. trichotis* localities follow Voss, 1988).

C. trichotis
1: Buena Vista, Tachira Andes, Venezuela (ca. 7 26 N, 72 26 W)
2: San Cristobal, Cordillera Oriental, Colombia (4 35 N, 74 05 W)
3: Cundinamarca, Cordillera Oriental, Colombia (4 36 N, 74 05 W)
4: Cordillera Carpish, Depto. Huanaco, Peru (ca. 9 40 S, 76 09 W)

C. sp. nov.
4: Cajas Plateau, Azuay Province, Ecuador. (2 50 S, 79 30 W)

be sure. If the southern population of *C. trichotis* do form a validly separate taxon then it would join a number of other taxa which have a separate sister species, or sub-species, whose distribution is centred on the Carpish Mountains (see CRACRAFT 1985; PARKER et al. 1985; ROBBINS et al. 1994), a situation paralleling that found in Cajas. These include the amethyst-throated Sunangel (*Heliangelus amethysticollis*) (d'Orbigny and Lafresnage, 1838), a high-altitude hummingbird with sub-species in Tachira, Bogota, south-western Ecuador and north-central Peru (FJELDSA and KRABBE 1990), and the chestnut-bellied cotinga (*Doliornis remseni* Robbins, Rosenberg, and Sornoza Molina, 1994) (see ROBBINS et al. 1994).

The Cajas Plateau is some distance from the other sites where specimens of *Chibchanomys* have been taken (around 940 km south from Bogota and 1000 km north from Huanuco). Similar disjunct distributions also occur in other ichthyomyine genera (Voss 1988). Such patterns are likely to be the result of dispersion in the minor interglacials, subsequent isolation and extinction of intervening populations in the cooler and drier periods of the four major Andean Pleistocene glaciations, with the current absence of species from wide areas of apparently suitable habitat resulting from the habitat preferences and

physiological limitations of Holocene forms, which have inhibited recolonization. This type of explanation was advanced by Chapman (1926) to account for disjunctions in the distribution of high Andean birds and has, with modifications, been used by many subsequent authors, over a wide range of taxa (Fjeldsa and Krabbe 1990; Vuilleumier and Monasterio 1986).

The coverage of small mammal collecting in the Andes is still patchy and there are many areas which are unexplored or little known (Reig 1986; Voss 1988; Carleton and Musser 1989). However, most of the mountains in the Ecuadorian Andes (e.g. Chimborazo, near Banos; Pichincha, near Quito) have been quite well trapped, and most include ichthyomyines amongst their known fauna. It is thus unlikely that the apparent geographical restriction of *Chibchanomys* sp. nov., and the absence of *C. trichotis*, are artefactual and it is highly probable that the new species of *Chibchanomys* is restricted to the Cajas Plateau, or (probably) the Serra de Machangara as a whole. However, range extensions for ichthyomyines are still being reported (Velasco Abad and Alberico 1984), so it may be premature to consider any such conclusions definitive at this time (in this context, compare, for example, distributional data for *Rheomys* from Hooper 1968 and Voss 1988). It is hoped the field key to known Ecuadorian Ichthyomyini (to be presented with the species' full description) will assist further work in this regard.

If *Chibchanomys* sp. nov. were to be found to be endemic to the Cajas Plateau/Serra Machangara, it would join the marsupial *Caenolestes tatei* Anthony, 1923 (Barnett 1991), two rodent sub-species *Phyllotis haggardi fuscus* Pearson, 1958 and *Thomasomys gracilis hudsoni* Anthony, 1923 (Cabrera 1961; Pearson 1958), the hummingbirds *Metallura baroni* Salvin, 1893 (Meyer de Schauensee 1966; Ortiz-Crespo 1984; Fjeldsa and Krabbe 1990) and *Coelogena iris hesperis* (Gould, 1853) (Meyer de Schauensee 1966; Fjeldsa and Krabbe 1990), an *Eleutherodactylus* frog (William Duellman, pers. comm.), a species of *Oroperipatus* (Onychophora) (Morley Read, pers. comm. 1988), the rove beetle genus *Cajachara* and a variety of as-yet-undescribed staphylinid beetles (Ashe and Leschen 1995), the puyas (Bromeliaceae) *Puya pygmea* L. B. Smith, 1952 and *P. nutans* L. B. Smith, 1952 (Gilmartin 1972; Gentry 1977) and the tillandsias (Bromeliaceae) *Tillandsia cuccullata* L. B. Smith, 1958, *T. rupicola* Baker, 1888, *T. pachyaxon* L. B. Smith, 1958, *T. buseri nubicola* Gilmartin, 1968, and *T. stenoura mauroi* Gilmartin, 1968 (Gilmartin 1972). All of these taxa are restricted to this outlier of the Western Cordillera.

Speciation patterns resulting in clusters of endemics on particular mountains or mountain chains are quite common in Andean Ecuador. For example, Mt. Pichincha has two endemic sub-species of rodent (*Phyllotis h. haggardi* Pearson, 1958; *Aepomys lugens vulcani* Thomas, 1890), an endemic hummingbird species (black-breasted puffleg *Eriocnemis nigrivestris* Bourcier and Mulsant, 1852) and several endemic sub-species (tourmaline sunangel *Helianthus e. exortis* Fraser, 1846; tryrian metaltail *Metallura tyrianthina quitensis* Loddges, 1832; glowing puffleg *Eriocnemis vestitus paramillo* Lesson, 1838). While subspecies of the Chimborazo hillstar (*Oreotrochilus estrella soderstromi* d'Orbigny and Lafresnage, 1838) and a rodent (*Phyllotis h. elegantulus* Pearson, 1958) are confined to Mt. Cotopaxi, (bird data: Meyer de Schauensee 1966; Fjeldsa and Krabbe 1990; rodent data: Cabrera 1961). Parallel patterns of restricted distribution are also found in many bromeliads (Gilmartin 1972).

Conservation

As pointed out by Happel et al. (1987), rarity is a composite term, comprising of low population density and restricted range. *Chibchanomys* sp. nov. appears to fulfil both of these criteria. Though allowance must be made for the fact that ichthyomyines are known to be difficult to trap (Musser and Gardner 1974; Voss 1988), *Chibchanomys* sp. nov.

would appear to favour a limited range of habitats and be uncommon within them. As trapping in neighbouring montane forest streams has had no success, the species is very likely to be restricted to streams in paramo vegetation, Happel et al. (1987) have shown that species with low densities, and restricted ranges and habitat preferences are those most vulnerable to extinction.

In addition to *Chibchanomys*, the Cajas Plateau has other rare small mammals (Barnett 1991, 1992), and a number of rare and/or restricted vertebrates, invertebrates and flowering plants. In Ecuador, tourism has increased greatly in the last few years (Boo 1990), and the Cajas Plateau area has become increasingly popular with visitors (Steven Leftwich, pers. comm.). A major road has recently been completed across the plateau and, as also noted by Ashe and Leschen (1995), this may increase the visitor volume to the point where "it is possible that Cajas may be(come) severely impacted by human activity in the near future". The negative environmental impacts of large numbers of visitors on high altitude areas is well known (Meyer 1993; Young et al. 1994; Andersen 1995; Eber 1992 for impacts on high-altitude terrestial ecosystems, Suren 1994; Ward 1994; Winterbourn 1994; Allen 1995 for impacts on high-altitude aquatic ecosystems and Kemf 1993 for a general overview). Consequently, the status and environmental health of the Cajas region should be monitored to ensure the survival of its endemic fauna and flora are not threatened. This may be further encouraged by community-orientated habitat preservation and ecotourism initiatives (Boo 1990).

Acknowledgements

I would like to thank Sergio Figeroa, Fernando Ortiz Crespo, Luis Albuja, (the late) Gustavo Orces, Francisco Escandon, and Pablo Vientimillia for institutional support and encouragement during fieldwork in Ecuador. Rose Ainesworth, Andrea Pogson, Caroline Lees, Steven Leftwich, Morley Read, and William Duellman very kindly provided unpublished field data. I am grateful to Fif Robinson, Jon Wright, Martin Perry, Robert Voss, the librarians at the Zoological Society of London and the staff of the Mammal Section, Natural History Museum, London.

Madeleine Prangley, Douglas and Chris Brandon-Jones, Becca Shapley commented on earlier versions of the manuscript. Traute and Rose Donno provided the Zusammenfassung. Jim and Teresa Clare generously allowed their unpublished observations of *Chibchanomys* to be used. Chris Brandon-Jones did the map.

Fieldwork in Ecuador was supported by grants from the British Ecological Society, Fauna and Flora Preservation Society, Royal Geographical Society, Percy Sladen Memorial Fund, the Twenty Seven Foundation and many others.

Zusammenfassung

Über Ökologie und Naturgeschichte einer fischenden Maus Chibchanomys spec. nov. (Ichthyomyini: Muridae) aus den Anden des südlichen Equador.

Über Habitat, Nahrung, Biogeographie und Erfordernissen zur Arterhaltung einer neuen Art des Genus *Chibchanomys* aus den Anden des südlichen Equador wird berichtet. Diese Art lebt an Bachsystemen des Paramo, ist sehr selten und ernährt sich wahrscheinlich hauptsächlich von größeren aquatischen Invertebraten aber auch von Fischen. Die Augen dieser Nager sind verkleinert, Vibrissen und deren Nerven stark entwickelt. Beobachtungen an einem gefangenen Individuum lassen vermuten, daß optische Leistungen bei der Nahrungssuche weitgehend durch Tasten ersetzt werden. Diese Art der Gattung *Chibchanomys* kommt in Höhen von 4 000 m vor und ist somit der am höchsten lebende Vertreter der Familie. Gemeinsam mit einigen anderen Wirbeltieren, Wirbellosen und Pflanzen ist dieser Nager ausschließlich auf dem Cajas Plateau Equador verbreitet. In einem Überblick wird auf Gefahren hingewiesen, die der gesamten endemischen Flora und Fauna dieses Plateaus drohen.

References

ALI, S. R. (1968 a): Bottom fauna of the streams and rivers of Hazara District after summer rains. Pakistan J. Sci. Ind. Res. **11**, 208–211.

ALI, S. R. (1968 b): Bottom fauna of the streams and rivers of Kohat District and Kurram Agency after winter rains. Pakistan J. Sci. Ind. Res. **11**, 449–453.

ALLEN, J. D. (1995): Stream Ecology: structure and function of running waters. London: Chapman and Hall.

ANDERSEN, U. V. (1995): Resistance of Danish coastal vegetation types to human trampling. Biol. Conserv. **71**, 223–230.

ASHE, J. S.; LESCHEN, R. A. B. (1995): *Cajachara carltoni*, a new Aleocharinae from an Ecuadorian paramo. Trop. Zool. **8**, 85–93.

BARNETT, A. A. (1991): Records of the grey-bellied shrew opossum, *Caenolestes caniventer* and Tate's shrew opossum, *Caenolestes tatei* (Caenolestidae, Marsupialia) from Ecuadorian montane forests. Mammalia **55**, 443–445.

BARNETT, A. A. (1992): Notes on the ecology of *Cryptotis montivaga* Anthony, 1921 (Insectivora, Soricidae), a high-altitude shrew from Ecuador. Mammalia **56**, 587–592

BARNETT, A. A.; DUTTON, J. (1995): Small Mammals (excluding bats). Expedition Advisory Centre, Expedition Field Techniques series. London: Expedition Advisory Centre Royal Geogr. Soc.

BOO, E. (1990): Ecotourism: the potentials and pitfalls. Vol. 2: case studies. Washington: World Wildlife Fund-US and US Agency Internat. Develop.

CABRERA, A. (1961): Catologo de los mamiferos de America del Sur. Rev. Mus. Cienc. Nat. "Bernardino Rivadavia" **4**, 309–732.

CARLETON, M. D; MUSSER, G. G. (1989): Systematic studies of oryzomine rodents (Muridae, Sigmodontinae): a synopsis of *Microryzomys*. Bull. Am. Mus. Nat. Hist. **191**, 1–83.

CHAPMAN, F. M. (1926): The distribution of bird-life in Ecuador: a contribution to a study of the origin of Andean bird-life. Bull. Am. Mus. Nat. Hist. **55**, 1–793.

CHURCHFIELD, S. (1985): The feeding ecology of the European water shrew. Mammal Rev. **15**, 13–21.

CRACRAFT, J. (1985): Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithol. Monogr. **36**, 49–84.

EBER, S. (ed.) (1992): Beyond the Green Horizon: a discussion paper on the principles of sustainable tourism. Godalming: World Wide Fund for Nature-UK and London: Tourism Concern.

ENDERS, R. K. (1939): A new rodent of the genus *Rheomys* from Chiriqui. Proc. Acad. Nat. Sci. Phila. **90**, 295–296.

FAIRLEY, J. S. (1972): Food of otters (*Lutra lutra*) from Co. Galway, Ireland, and notes on other aspects of their biology. J. Zool. (London) **166**, 469–474.

FJELDSA, J.; KRABBE, N. (1990): Birds of the High Andes. Zool. Mus., Univ. Copenhagen, Svendborg: Apollo Books.

GENTRY, A. H. (1977): Endangered plant species and habitats of Ecuador and Amazonian Peru. In: Extinction is Forever: the status of threatened and endangered plants of the Americas. Ed. by G. T. PRANCE and T. S. ELIAS. New York: The New York Botanical Garden. Pp. 136–149.

GILMARTIN, A. J. (1972): The Bromeliaceae of Ecuador. Phanerogamarum Monogr. **4**, 1–255.

GIRAUDOUX, P.; PRADIER, B.; DELATTRE, P.; DEBLAY, S.; SALVI, D.; DEFAUT, R. (1995): Estimation of water vole abundance by using surface indices. Acta Theriol. **40**, 77–96.

HAPPEL, R. E.; NOSS, J. F; MARSH, C. W. (1987): Distribution, abundance and endangerment of Primates. In: Primate Conservation in the tropical Rain Forest. Ed. by C. W. MARSH and R. A. MITTERMEIER. Monographs in Primatology. Vol. 9, New York: Alan R. Liss. Pp. 63–82.

HOOPER, E. T. (1968): Habitats and food of amphibious mice of the genus *Rheomys*. J. Mammalogy **49**, 550–553.

KEMF, E. (1993): Indigenous Peoples and Protected Areas. London: Earthscan Publ. Ltd.

MEYER, E. (1993): Beeinflussung der Fauna alpiner Böden durch Sommer- und Wintertourismus in West-Österreich. Rev. Suisse Zool. **100**, 519–527.

MEYER DE SCHAUENSEE, R. (1966): The Species of Birds of South America and Their Distribution. Philadeliphia: Acad. Nat. Hist.

MUSSER, G. G.; GARDNER, A. L. (1974): A new species of the ichthyomyine *Daptomys* from Peru. Am. Mus. Novitates **2537**, 1–23.

NIELSEN, A. (1950): The torrential invertebrate fauna. Oikos **2**, 177–196.

OCHOA, G. J.; SORIANO, P. (1991): A new species of water rat, genus *Neusticomys* Anthony, from the Andes of Venezuela. J. Mammalogy **72**, 97–103.

Ormerod, S. J.; Rundle, S. D.; Wilkinson, S. M.; Daly, G. P.; Dale, K. M.; Juttner, I. (1994): Altitudinal trends in the diatoms, bryophytes, macroinvertebrates and fish of a Nepalese river system. Freshwater Ecol. **32**, 309–322.

Ortiz-Crespo, F. I. (1984): First twentieth-century specimen of the Violet-throated Metaltail (*Metallura baroni*). Bull. Br. Ornithol. Club **104**, 95–97.

Parker, T. A. III; Schulenberg, T. S.; Graves, G. R.; Braun, M. J. (1985): The avifauna of the Huancamba region, northern Peru. Ornithol. Monogr. **36**, 169–197.

Pearson, O. P. (1958): A taxonomic revision of *Phyllotis*. Univ. Calif. Pub. Zool. **56**, 391–457.

Ramsay, P. M. (1992): The Paramo Vegetation of Ecuador. PhD Thesis. Bangor: Univ. College North Wales.

Reig, O. (1986): Diversity patterns and differentiation of high Andean rodents. In: High Altitude Tropical Biogeography. Ed. by F. Vuilleumier and M. Monasterio. Oxford: University Press. Pp. 404–439.

Robbins, M. B.; Rosenberg, G. H.; Sornoza Molina, F. (1994): A new species of cotinga (Cotingae: *Doliornis*) from the Ecuadorian Andes, with comments on plumage sequences in *Doliornis* and *Amplion*. The Auk **111**, 1–7.

Starrett, A.; Fisler, G. F. (1970): Aquatic adaptations of the water mouse; *Rheomys underwoodi*. Los Angeles County Museum, Contrib. Sci. **182**, 1–1.

Stirton, R. A. (1944): Tropical mammal trapping I: the water mouse *Rheomys*. J. Mammalogy **25**, 337–343.

Suren, A. M. (1994): Macroinvertebrate communities of streams in eastern Nepal: effects of altitude and land use. Freshwater Biol. **32**, 323–336.

Tate, G. H. H. (1931): Random observations on habits of South American mammals. J. Mammalogy **12**, 248–256.

Thomas, O. (1893): On some mammals from central Peru. Proc. Zool. Soc. Lond. **1893**, 333–341.

Turcotte, P.; Harper, P. P. (1982): The macroinvertebrate fauna of a small Andean stream. Freshwater Biol. **12**, 411–419.

Velasco Abad E.; Alberico, M. (1984): Notas sobre algunos mamiferos nuevos e a fauna Vallecaucana. Cespedesia **13**, 291–295.

Voss, R. S. (1988): Systematics and ecology of ichtyomyine rodents (Muroidea): patterns of morphological evolution in a small adaptive radiation. Bull. Am. Mus. Nat. Hist. **188**, 259–493.

Voss, R. S.; Silva, J. L.; Valdes, L., J. A. (1982): Feeding behavior and diets of Neotropical water rats, genus *Ichthyomys* Thomas, 1893. Z. Säugetierkunde **47**, 364–369.

Vuilleumier, F.; Monasterio, M. (1986): High Altitude Tropical Biogeography. Oxford: Univ. Press.

Ward, J. V. (1994): Ecology of alpine streams. Freshwater Biol. **32**, 277–294.

Wilson, D. E.; Reeder, D. M. (1993): Mammal Species of the World: A Taxonomic and Geographic Reference. Washington, London: Smithsonian Inst. Press.

Winterbourne, M. J. (1994): Ecology of alpine, glacial, high latitude and mountain streams: introduction and synthesis. Freshwater Biol. **32**, 235–239.

Woodall, P. F. (1993): Dispersion and habitat preference of the Water Vole (*Arvicola terrestris*) on the River Thames. Z. Säugetierkunde **58**, 160–171.

Woollard, P.; Vestjens, W. J. M.; MacLean, L. (1978): The ecology of the eastern water rat *Hydromys chyrogaster* at Griffith, N.S.W.: food and feeding habits. Aust. Wildl. Res. **5**, 59–73.

Young, R. G.; Huryn, A. D.; Townsend, C. R. (1994): Effects of agricultural development on processing of tussock leaf litter in high country New Zealand streams. Freshwater Biol. **32**, 413–427.

Author's address: Adrian A. Barnett, c/o Dr. H. Box, Department of Psychology, University of Reading, 3 Earley Gate, Whiteknights, Reading RG6 6Al, United Kingdom.

Z. Säugetierkunde **62** (1997) 53–57

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Y Chromosome Polymorphism in the Bank vole *Clethrionomys glareolus* (Rodentia, Mammalia)

By M. Vujošević and Jelena Blagojević

Department of Genetics, Institute for Biological Research "Siniša Stanković", Belgrade, Yugoslavia

Receipt of Ms. 10. 04. 1996
Acceptance of Ms. 06. 06. 1996

The genus *Clethrionomys* is characterized by a uniform karyotype concerning number and morphology of chromosomes and also G-bands distribution (Nadler et al. 1976; Zima and Kral 1984; Yoshida et al. 1989). All species examined had the same diploid number $2n = 56$ with all chromosomes being acrocentric of gradually decreasing size except one pair of small metacentrics, thus FNa being 56. In all species the X chromosome is among the largest acrocentrics in the karyotype. The only differences at the chromosomal level found between species and populations concern the morphology of the Y chromosome. Yoshida et al. (1989) found three types of Y chromosome in 7 species of the genus *Clethrionomys* from Japanese islands. In the bank vole, *Clethrionomys glareolus* the Y chromosome is a small metacentric in most cases (Matthey and Renaud 1935; Hsu and Benirschke 1970; Vorontsov et al. 1978). However, Savić et al. (1968) and Živković et al. (1975) found acrocentric Y chromosomes in some specimens from former Yugoslavia. Acrocentric Y chromosomes were also found by Kral et al. (1972) at Monte Gargano, Italy, which led them to the conclusion that two types of Y chromosomes are connected with the distribution of different subspecies. However, Radosavljević et al. (1988) found animals in one population on Jastrebac mountain in former Yugoslavia with acrocentric and submetacentric Y chromosomes. The aim of this study was to further investigate polymorphism of the Y chromosome in this species.

A total of 80 males of *Clethrionomys glareolus* were caught in "Longworth" traps at the following localities in former Yugoslavia: Cer (CQ84) 17, Jastrebac (EP30) 27, Goč (DP82) 5, Kopaonik (DN88) 17, Mokrec (VL68) 3, Snježnik (VL63) 1, Šara (EM06) 5, Travna Gora (VL76) 3, Tara (CP66) 2 (Coordinates of UTM system are given in brackets). Chromosome preparation was done directly from bone marrow using standard procedure. G-bands were obtained according to the modified schedule of Seabright (1971) and C-bands with an adopted method of Summer (1972). Chromosome analyses where done on 20 metaphases for each specimen.

All animals studied had the same karyotype $2n = 56$ and NFa = 56. Differences were established only in the morphology of the Y chromosome. Y chromosomes were among the smallest in the karyotype, being about one-fourth of the X chromosome size. Two types of Y chromosomes were found (Tab. 1). The metacentric type was found in 47 animals (58.8%) and remaining 41.2% had acrocentric Y chromosomes. Both types of Y chromosomes appeared almost entirely heterochromatic after C-banding (Fig. 1). G-bands did not provide any further information about differences between the two types of Y chromosomes due to their small size.

Table 1. Types of Y chromosomes in *Clethrionomys glareolus* at different localities (f-m – frequency of metacentric Y).

Locality	metacentric Y	acrocentric Y	N	f-m
1. Mokrec	–	3	3	0.00
2. Snježnik	–	1	1	0.00
3. Travna Gora	–	3	3	0.00
4. Cer	3	14	17	0.18
5. Goč	2	3	5	0.40
6. Šara	4	1	5	0.80
7. Jastrebac	22	5	27	0.81
8. Kopaonik	14	3	17	0.82
9. Tara	2	–	2	1.00
Total	**47**	**33**	**80**	**0.59**

Three localities were represented with a greater number of animals (Kopaonik, Jastrebac and Cer) and in all of them intrapopulational polymorphism of the Y chromosome was present. At Kopaonik and Jastrebac metacentrics predominated (Fig. 2). The frequency of metacentrics was 0.81 for Jastrebac and 0.82 for Kopaonik. However, the ratio of metacentric (0.18) and acrocentric chromosomes at Cer differed significantly from those at Kopaonik ($X^2 = 4.24$, $p < 0.001$) and Jastrebac ($X^2 = 7.33$, $p < 0.001$). Although the samples from Šara and Goč were considerably smaller, the presence of the two forms was also revealed. At three localities from northwest only acrocentrics were found, while Tara was characterized by metacentrics only.

In most of the cases where polymorphism of the Y chromosome was found in mammals the size of the Y chromosome and the amount of constitutive heterochromatine was variable. This phenomenon is well-known in man (BORGOANKAR 1977), and in some rodents as well.

In the genus *Clethrionomys* polymorphism of the Y chromosome is connected with different morphological forms. Besides *C. glareolus*, different types of Y chromosomes, acrocentric and metacentric, characterize populations of *C. rutilus* and *C. rufocanus*. In both species the metacentric type predominates. In *C. rutilus* acrocentrics were found only in populations south of Siberia (VORONTSOV et al. 1978). Acrocentric Y chromosomes characterize populations of *C. rufocanus* from Japanese islands (HSU and BENIRSCHKE 1969; YOSHIDA et al. 1989), Mongolia (ORLOV et al. 1978) and Sweden (GAMPERL 1982). However, on the Japanese islands differences occur at the species level in the 7 species of *Clethrionomys* (YOSHIDA et al. 1979). Three of them are characterized by metacentric Y, other three by acrocentric and only one by subtelocentric Y. No intraspecific variation of Y was found. A dendrogram constructed from allozyme data for these species was consistent with the distribution of the variants of the Y chromosome.

In *C. glareolus*, like in *C. rutilus* and *C. rufocanus* the acrocentric form of Y chromosome is limited in its distribution. Besides some parts of former Yugoslavia it includes only Monte Gargano in Italy. VORONTSOV et. al. (1980) concluded that the variants of Y are fixed in isolated populations near the borders of species ranges. We found populations with one form of Y (acrocentric) only in the northwest part of ormer Yugoslavia. All others, except one, had two types of Y. Metacentric Y predominate in all samples except on Cer which is closest to the northwest localities.

There exists a trend of increase of metacentric Y chromosomes from the northwest to the southeast.

It could be supposed that the presence of different types of Y chromosomes at the same localities resulted from a secondary contact of previously isolated populations (or subspecies). This contact may have been a postglacial event.

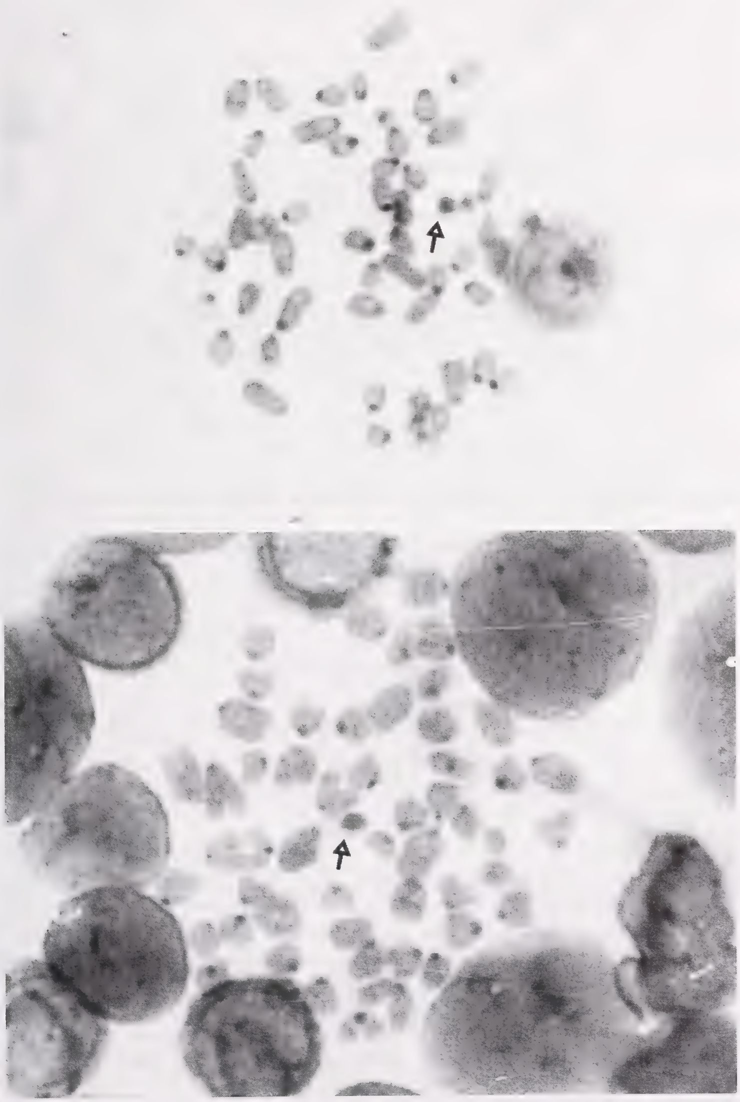


Fig. 1. C-banded metaphases of *C. glareolus* with metacentric (a) and acrocentric (b) Y chromosome (marked with asterisk).

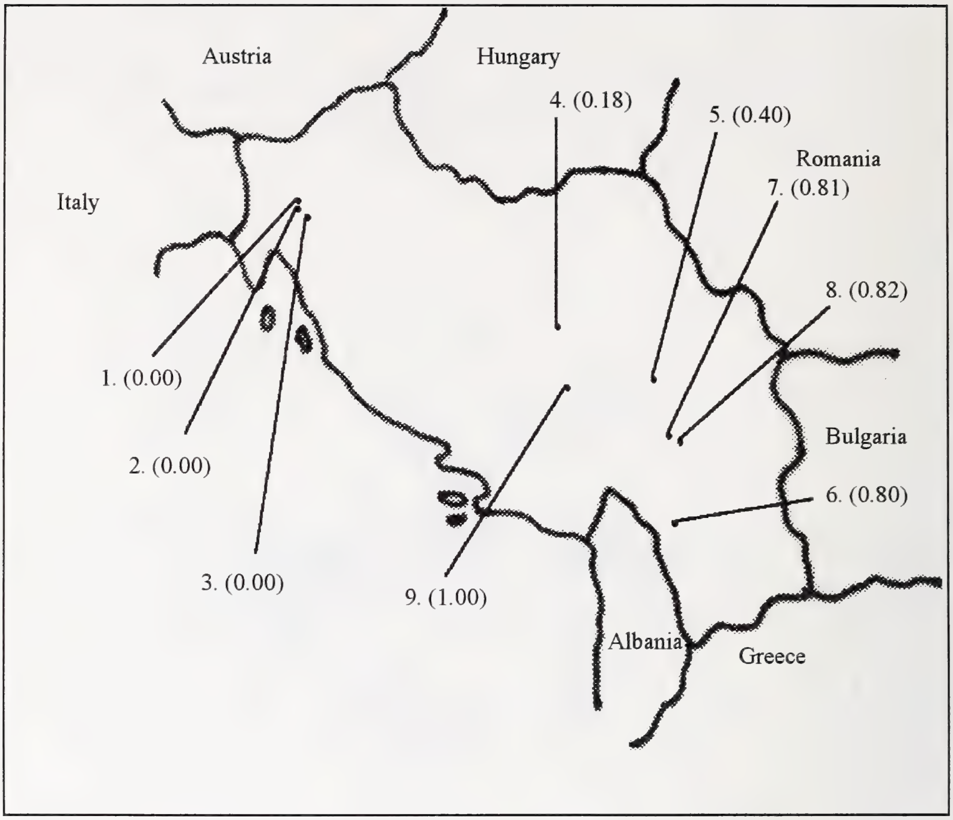


Fig. 2. Frequency of metacentric Y chromosomes at different localities in former Yugoslavia (names of localities given in Tab. 1).

Acknowledgement

Supported by the Ministry of Science and Technology of Serbia, contract No. 0322.

References

Borgaonkar, D. S. (1977): Chromosomal variation in man. A catalog of chromosomal variants and anomalies. 2nd ed. New York: Alan R. Liss. Pp. 3–402.

Gamperl, R. (1982): Chromosomal evolution in the genus *Clethrionomys*. Genetica **57**, 193–197.

Hsu, T. C.; Benirschke, K. (1970): An atlas of mammalian chromosomes, Vol. III, IV, Berlin, Heidelberg, New York: Springer-Verlag.

Kral, B.; Lehmann, E. von; Zejda, J. (1972): Die Hybriden zweier Unterarten der Rötelmaus (*Clethrionomys glareolus* Schreb.). Zool. Listy **21**, 43–61.

Matthey, R.; Reund, P. (1935): Le type de digametic male et les chromosomes chez deux campagnols. Comp. Rend. Sean. Soc. Biol. **120**, 595.

Nadler, C. F.; Rausch, V. R.; Lyapunova, E. A.; Hoffmann, R. S.; Vorontsov, N. N. (1976): Chromosomal banding patterns of Holarctic rodents, *Clethrionomys rutilus* and *Microtus oeconomus*. Z. Säugetierkunde **41**, 137–146.

Orlov, V. N.; Radjabli, S. I.; Malygin, V. M.; Chotolchu, N.; Kovalskaja, Y. M.; Bulatova, N. Š.; Baskevič, M. I. (1978): Karyotypes of the mammals from Mongolia. Moscow: Nauka. Pp 149–164 (in Russian).

Radosavljević, J.; Vujošević, M.; Živković, S. (1988): Intrapopulation variability of the Y chromosome in the Bank vole (*Clethrionomys glareolus* Schreber, 1880). Arh. biol. nauka (Beograd) **40**, 3P–4P.

Savić, I.; Soldatović, B.; Đulić, B. (1968): Karyotype of the species *Clethrionomys glareolus* Schreber, 1780 (Microtinae, Rodentia) in Bačka. Arh. biol. nauka. (Belgrade) **20**, 1P–2P.

Seabright, M. (1971): A rapid banding technique for human chromosomes. Lancet **11**, 971–972.

Summner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exp. Cell Res. **75**, 304–306.

Vorontsov, N. N.; Lyapunova, E. A.; Ivanckaja, E. Ju.; Nadler, C. F.; Kral, B.; Kozlovskij, A. I.; Hoffmann, R. S. (1978): Variability of sex chromosomes in mammals I. Geographical variability of morphology of Y chromosome in voles of the genus *Clethrionomys* (Rodentia, Microtinae). Genetika **14**, 1432–1446.

Vorontsov, N. N.; Lyapunova, E. A.; Borissov, Yu. M.; Dovgal, V. E. (1980): Variability of sex chromosomes in mammals. Genetica **52/53**, 361–372.

Yoshida, I.; Obara, Y.; Matsuoka, N. (1989): Phylogenetic relationships among seven taxa of the Japanese microtinae voles revealed by karyological and biochemical techniques. Zool. Sci. **6**, 409–420.

Zima, J.; Kral, B. (1984): Karyotype of European mammals II. Acta Scientarium Naturalum Academiae Scientarum Bohemoslovacae (Brno) **18**, 1–62.

Živković, S.; Petrov, B.; Soldatović, B.; Savić, I. (1975): Two morphologically different Y chromosomes in the Bank vole (*Clethrionomys glareolus*, Schreb.) from Serbia (Yugoslavia). Acta Vet. **25**, 241–246.

Authors' address: Dr. Mladen Vujošević and Jelena Blagojević, Department of Genetics, Institute for Biological Research, 29 Novembra 142, 11060 Belgrade, Yugoslavia.

Z. Säugetierkunde 62 (1997) 58–62

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Are feral house mice from the sub-Antarctic adapted to cold?

By P. I. Webb, G. T. H. Ellison, J. D. Skinner, and R. J. Van Aarde

Mammal Research Institute, University of Pretoria, Pretoria, South Africa.

Receipt of Ms. 19. 06. 1996
Acceptance of Ms. 28. 09. 1996

In small mammals adaptation to cold environments may be expressed in the form of elevated basal metabolic rate (BMR) (eg Buffenstein and Jarvis 1985), reduced minimum thermal conductance (eg Casey et al. 1979), and/or elevated maximum non-shivering thermogenesis (NST) (eg Haim and Izhaki 1993). Marion Island (46° 54′ S, 37° 45′E) lies in the sub-Antarctic and has one of the most oceanic climates in the world (Smith and Steenkamp 1990); mean surface air temperature is 5.7 °C (Smith and Steenkamp 1990) while seasonal variation in mean surface air temperature is only about 4.1 °C (Smith 1987). House mice (*Mus musculus*) were introduced to Marion Island at least 170 years ago (Berry et al. 1978), a time in which we might expect the passage of at least 300–400 generations. Such a period is certainly long enough for significant shifts in population genetics to occur. For example wild caught house mice bred for only 9 generations in the cold and then returned to a warm environment have been shown to be superior to controls in reproductive performance and growth (Barnett et al. 1975). Also seasonal changes in heterozygosity in 3 out of 6 loci and genetic variation that was higher than expected for a small founder population have been taken as evidence for natural selection in an island population of house mice (Berry and Murphy 1970; Berry and Peters 1977) as has age related genetic variation in Marion Island mice (Berry et al. 1973). Physiological parameters associated with thermoregulation have previously been shown to have low heritability (<0.1) in house mice (Lacy and Lynch 1979), lower for instance than body mass (circa 0.4) or aspects of thermoregulatory behaviour such as nesting (circa 0.3) (Lacy and Lynch 1979). Such differences in heritability are verified by the presence or absence of clinal variation in such parameters in the wild (Lynch 1992). However it has been suggested that due to the harshness of the climate, *M. musculus* on Marion Island are living close to their physiological limit (Berry et al. 1978) implying that selective pressure on thermoregulatory physiology in this population will be high. In this study we compare aspects of thermoregulatory physiology in adult *M. musculus* from Marion Island with allometric predictions from other murid and mammal species and with previous measures from other feral *M. musculus* populations and laboratory stocks. Our intention is to establish the presence or absence of adaptation of thermoregulatory physiology to the harsh Marion Island climate.

Feral adult *M. musculus* were live-trapped on Marion Island, maintained individually in cages in a climate chamber at the University of Pretoria and acclimated at constant temperature under a 12L:12D photoperiod for at least six weeks prior to the onset of experimentation. Food and water were available ad lib. Shredded tissue paper and sawdust were provided for bedding.

Standard metabolic rate (SMR) of individuals of known body mass was determined by measuring minimum oxygen consumption at 11 ambient temperatures ranging from 0 to 35 °C using open-flow respirometry. At each temperature measurements were made on

five or six individuals randomly selected from a pool of 14 mice acclimated to 23 °C. SMR of a given mouse at a given ambient temperature was taken as the mean of the lowest five consecutive measures of oxygen consumption over a 2 hour period. At the end of the 2 hour period body temperature was taken by inserting a thermocouple 1 cm into the rectum. All measures of SMR were corrected to standard temperature and pressure of dry air. The thermoneutral zone was defined as the range of ambient temperature within which mean SMR (ie across all individuals) was minimal and independent of ambient temperature. Mean oxygen consumption within the thermoneutral zone was taken to represent basal metabolic rate (BMR). Thermal conductance was calculated as oxygen consumption during the last five minutes of the 2 hour measurement period divided by the body-ambient temperature differential. For each individual the lowest measure of thermal conductance at temperatures below the thermoneutral zone was taken to represent minimum thermal conductance. Maximum non-shivering thermogenesis (NST) was determined as maximum thermogenic response (oxygen consumption) to nor-adrenaline following the procedure of Ellison and Skinner (1991) in six mice acclimated to low temperature (5 °C) (Heldmaier 1971). All measures of oxygen consumption were converted to Watts by assuming a calorific equivalence of oxygen of 20.1 $W.ml^{-1}$ (for a non-protein RQ of 0.8; Elia and Livesey 1988).

Values of BMR, minimal thermal conductance and NST were compared with predictions from body mass based on allometric equations generated through log-log model I regression analysis of previously published data (Data used in regression analysis were as follows; BMR: 59 species of Muridae from Hayssen and Lacy 1985; Minimum thermal conductance: 19 species of Muridae from Bradley and Deavers 1980; NST: 25 species of Rodentia from Haim and Izhaki 1993). A measure was said to be significantly different to its predicted value if it fell outside the 95% confidence interval of the prediction.

BMR was significantly lower while minimum thermal conductance was exactly the same as the respective allometrically predicted values (Tab. 1). Once body mass differences had been accounted for by quoting all data as a proportion of allometrically predicted values, BMR also fell below that recorded in all laboratory populations of house mice and all other populations of feral house mice considered, although only marginally in the case of a feral population from Wisconsin (Tab. 1). Minimum thermal conductance also fell below that recorded in all laboratory or feral populations considered, although again the differences were marginal for two laboratory populations (Tab. 1). NST was significantly higher than the allometric prediction but was not consistently higher or lower than recorded in other populations of feral or laboratory house mice once differences in body mass had been accounted for (Tab. 1).

We therefore suggest that both BMR and minimum thermal conductance are comparatively low in *M. musculus* from Marion Island while NST is neither especially high or especially low. Low thermal conductance is consistent with genotypic or developmental adaptation to cold (Casey et al. 1979) but low BMR is not. The lack of a comparatively high NST is consistent with previous analyses of body composition; even though interscapular brown fat mass (per gram body mass) increases with decreasing meteorological temperature across feral house mouse populations (Jakobsen 1981), Marion Island mice have comparatively less interscapular brown fat than do house mice from Taunton in the south of England, or even than house mice from Hawaii (Berry et al. 1979). If *M. musculus* from Marion Island were physiologically adapted to cold we might expect them to demonstrate comparatively high NST.

However, low BMR is consistent with adaptation to limited food (and hence metabolisable energy) availability (McNab 1986; Webb and Skinner 1996). Evidence that food availability is a limiting factor for *M. musculus* population expansion on Marion Island is circumstantial but implied by the coincidence of high mortality and declining food avail-

Table 1. Thermoregulatory physiological parameters in *Mus musculus*. BMR – basal metabolic rate. NST – non-shivering thermogenesis. Predicted values were calculated allometrically from log-log model I regressions of previously published data. See text for further details. Errors are ±1 standard deviation. Measures are ranked in descending order by % of predicted value

Parameter and reference	Population	Body mass (g)	Acclimation condidtions (°C)	Value Measured	% pre-dicted
BMR (Watts)					
GÓRECKI et al. (1990)	Poland	13.2	–	0.364	214
GÓRECKI and KANIA (1986)	laboratory	27	20	0.513	184
BARTKE and GÓRECKI (1968)	laboratory	30	?	0.536	179
GÓRECKI et al. (1990)	Bulgaria	18.6	–	0.274	128
JAKOBSEN (1978)	Isle of May	18.6	summer	0.225	104
HELDMAIER (1971)	laboratory	33.4	5	0.330	103
RICHARDSON et al. (1994)	laboratory	18.0	22	0.214	101
HUDSON and SCOTT (1979)	laboratory	45.5	20–24	0.373	94
Richardson et al. (1994)	Wisconsin	11.2	22	0.119	77
Present study	Marion Island	21.2 (±4.2)	23	0.171 (±0.025)	72
Minimum thermal conductance (Watts. °C^{-1})					
GÓRECKI and KANIA (1986)	laboratory	27.9	20	0.0497	181
JAKOBSEN (1978)	Isle of may	18.6	summer	0.0268	121
HUDSON and SCOTT (1979)	laboratory	45.5	20–24	0.0381	107
HART (1950)[a]	laboratory	26	?	0.0276	105
Present study	Marion Island	27.0 (±3.4)	23	0.0269 (±0.0073)	100
NST (Watts)					
RICHARDSON et al. (1994)	Wisconsin	11.5	22	0.886	399
RICHARDSON et al. (1994)	Laboratory	19.0	22	1.095	346
Present study	Marion Island	23.1 (±4.0)	5	1.136 (±0.231)	312
HELDMAIER (1971)	Laboratory	33.4	5	1.294	274
JAKOBSEN (1978)	Isle of May	18.6	summer	0.825	264

[a]) in BRADLEY and DEAVERS (1985)

ability in winter (GLEESON and VAN RENSBURG 1982; MATTHEWSON et al. 1994). *Mus musculus* from Marion Island are also comparatively small (BERRY et al. 1978) although they are both heavier and have relatively shorter tails than feral house mice from Macquarie Island, also in the sub-Antarctic (BERRY et al. 1978). Small body size will help reduce total energy demand. Finally, incidental observations on house mice from Marion Island indicate a tendency to hoard food when available in excess both in the field (R. J. VAN AARDE, unpubl. data) and in the laboratory (G. T. H. ELLISON, unpubl. data). This may represent a behavioural adaptation to short term fluctuations in food availability in the wild.

We suggest that *M. musculus* from Marion Island do show physiological adaptation to cold (via a reduction in minimum thermal conductance) but that limited availability of energy on the island has prevented adaptative changes that would have resulted in increased in energy demand (eg increased BMR or NST).

Acknowledgements

Financial and logistic support were provided by the University of Pretoria and the Foundation for Research Development in South Africa. SARA FREARS commented constructively on an earlier draft of the manuscript.

References

BARNETT, S. A.; MUNRO, K. M. H.; SMART, J. L.; STODDART, R. C. (1975): House mice bred for many generations in two environments. J. Zool. (London) **177**, 153–169.

BARTKE, A.; GÓRECKI, A. (1968): Oxygen consumption by obese yellow mice and their normal littermates. Am. J. Physiol. **214**, 1250–1252.

BERRY, R. J.; MURPHY, H. M. (1970): Biochemical genetics of an island population of the house mouse. Proc. R. Soc., Series B **176**, 87–103.

BERRY, R. J.; PETERS, J. (1977): Heterogenous heterozygosities in *Mus musculus* populations. Proc. R. Soc., Series B **197**, 485–503.

BERRY, R. J.; JAKOBSEN, M. E.; TRIGGS, G. S. (1973): Survival in wild-living house mice. Mamm. Rev. **3**, 46–57.

BERRY, R. J.; PETERS, J.; AARDE, R. J. VAN (1978): Sub-antarctic house mice: colonization, survival and selection. J. Zool. (London) **184**, 127–141.

BERRY, R. J.; BONNER, W. N.; PETERS, J. (1979): Natural selection in house mice (*Mus musculus*) from South Georgia (South Atlantic Ocean). J. Zool. (London) **189**, 385–398.

BRADLEY, S. R.; DEAVERS, D. R. (1980): A re-examination of the relationship between thermal conductance and body weight in mammals. Comp. Biochem. Physiol. **65 A**, 465–476.

BUFFENSTIEN, R.; JARVIS, J. U. M. (1985): Thermoregulation and metabolism in the smallest African gerbil, *Gerbillus pusillus*. J. Zool. (London) **205**, 107–121.

CASEY, T. M.; WITHERS, P. C.; CASEY, K. K. (1979): Metabolic and respiratory responses of arctic mammals to ambient temperature during the summer. Comp. Biochem. Physiol. **64 A**, 331–341.

ELIA, M.; LIVESEY, G. (1988): Theory and validity of indirect calorimetry during net lipid synthesis. Am. J. Clin. Nutr. **47**, 591–607.

ELLISON, G. T. H.; SKINNER, J. D. (1991): Thermoregulation and torpor in African woodland dormice, *Graphiurus murinus*, following cold acclimation. Z. Säugetierkunde **56**, 41–47.

GLEESON, J. P.; RENSBURG, P. J. J. VAN (1982): Feeding ecology of the house mouse *Mus musculus* on Marion Island. S. A. J. Ant. Res. **12**, 34–39.

GÓRECKI, A.; KANIA, Z. (1986): Maximum metabolism and thermoregulation in laboratory mice. Acta Theriol. **31**, 97–105.

GÓRECKI, A.; MECZEVA, R.; PIS, T.; GERASIMOV, S.; WALKOWA, W. (1990): Geographical variation of thermoregulation in wild populations of *Mus musculus* and *Mus spretus*. Acta Theriol. 35, 209–214.

HAIM, A.; IZHAKI, I. (1993): The ecological significance of resting metabolic rate and non-shivering thermogenesis for rodents. J. therm. Biol. **18**, 71–81.

HART, J. S. (1950): Interrelations of daily metabolic cycle, activity, and environmental temperature of mice. Can. J. Res., Section D **28**, 293–307.

HAYSSEN, V.; LACY, R. C. (1985): Basal metabolic rates in mammals: taxonomic differences in the allometry of BMR and body mass. Comp. Biochem. Physiol. **81 A**, 741–754.

HELDMAIER, G. (1971): Zitterfreie Wärmebildung und Körpergröße bei Säugetieren. Z. vergl. Physiologie **73**, 222–248.

HUDSON, J. W.; SCOTT, I. M. (1979): Daily torpor in the laboratory mouse, *Mus musculus* Var. Albino. Physiol. Zool. **52**, 205–218.

JAKOBSEN, M. E. (1978): Winter acclimatization and survival of wild house mice. J. Zool. (London) **185**, 93–104.

JAKOBSEN, M. E. (1981): Physiological adaptability: the response of the house mouse to variations in the environment. Symp. Zool. Soc. Lond. **47**, 301–335.

LACY, R. C.; LYNCH, C. B. (1979): Quantitative genetic analysis of temperature regulation in *Mus musculus*. I. Partitioning of variance. Genetics **91**, 743–753.

LYNCH, C. B. (1992): Clinal variation in cold adaptation in *Mus domesticus*: verification of predictions from laboratory populations. Am. Nat. **139**, 1219–1236.

MATTHEWSON, D. C.; AARDE, R. J. VAN; SKINNER, J. D. (1994): Population biology of house mice (*Mus musculus* L.) on sub-Antarctic Marion Island. S. A. J. Sci. **29**, 99–106.

MCNAB, B. K. (1986): The influence of food habits on the energetics of eutherian mammals. Ecol. Monogr. **56**, 1–19.

RICHARDSON, C. S.; DOHM, M. R.; GARLAND, T. (1994): Metabolism and thermoregulation in crosses between wild and random-bred laboratory mice (*Mus domesticus*). Physiol. Zool. **67**, 944–975.

SMITH, V. R. (1987): The environment and biota of Marion Island. South African J. **83**, 211–220.

SMITH, V. R.; STEENKAMP, M. (1990): Climate change and its ecological implications at a sub-antarctic island. Oecologia **85**, 14–24.
WEBB, P. I.; SKINNER, J. D. (1996): Physiological adaptation to aridity in the bushveld gerbil, *Tatera leucogaster*. J. Zool. (London) **238**, 693–701.

Authors' addresses: Dr. PETER I. WEBB, Department of Zoology, University of Otago, PO Box 56, Dunedin, New Zealand; Dr. GEORGE T. H. ELLISON, School of Biological and Chemical Sciences, University of Greenwich, London SE18 6PF, UK; Prof. JOHN D. SKINNER and Prof. RUDI J. VAN AARDE, Mammal Research Institute, University of Pretoria, Pretoria 0002, South Africa.

Z. Säugetierkunde **62** (1997) 63–64

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

MITTEILUNGEN DER GESELLSCHAFT

Einladung

Auf Einladung von Herrn Prof. Dr. M. S. Fischer und Herrn Prof. Dr. S. Halle, Jena, findet die 71. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde e. V. von Sonntag, dem 21. September, bis Donnerstag, dem 25. September 1997, an der Friedrich-Schiller-Universität in Jena statt.

Vorläufiges Programm

Sonntag, 21. September:	Anreise ab 16.00 Uhr: Vorstandssitzung im Seminarraum des Instituts für Spezielle Zoologie, Erbertstr. 1, D-07743 Jena. ab 19.00 Uhr: Zwangloser Begrüßungsabend im Hotel „Roter Hirsch", Holzmarkt 10, D-07743 Jena
Montag, 22. September:	09.00 Uhr: Großer Hörsaal des Zoologischen Instituts: Grußworte und Eröffnung der Tagung durch den 1. Vorsitzenden 09.30 Uhr: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Motorik bei Säugetieren" 14.00 Uhr: Posterdemonstration 15.00 Uhr: Kurzvorträge 17.00 Uhr: Mitgliederversammlung 20.00 Uhr: Empfang im Rathaus der Stadt Jena
Dienstag, 23. September:	09.00 Uhr: Großer Hörsaal des Zoologischen Instituts: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Methoden säugetierkundlicher Freilandforschung" 14.00 Uhr: Posterdemonstration 15.30 Uhr: Kurzvorträge 19.30 Uhr: Geselliger Abend
Mittwoch, 24. September:	09.00 Uhr: Großer Hörsaal des Zoologischen Instituts: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt: „Biologie der Musteliden" 14.00 Uhr: Posterdemonstration 15.30 Uhr: Kurzvorträge 18.00 Uhr: Posterprämierung
Donnerstag, 25. September:	09.00–17.00 Uhr: 1. Exkursion: Busfahrt nach Renthendorf zur Brehm-Gedenkstätte, Klosterruine Paulinzella und nach Weimar 2. Exkursion: Wanderung um Jena 09.00 Uhr–12.00 Uhr: Zool. Institut: Workshops/Symposien versch. Arbeitsgruppen

Die Vorträge und Posterdemonstrationen finden statt in den Räumen des Zoologischen Instituts der Friedrich-Schiller-Universität Jena, Erbertstr. 1, D-07743 Jena.

Alle Mitglieder und an der Säugetierforschung und dem Säugetierschutz interessierten Nichtmitglieder sind zu dieser Jahrestagung 1997 herzlich nach Jena eingeladen. Falls eine persönliche Einladung gewünscht wird, wenden Sie sich bitte an den 1. Vorsitzenden der Deutschen Gesellschaft für Säugetierkunde, Prof. Dr. H. Erkert, Zoologisches Institut, Morgenstelle 28, D-72076 Tübingen (Tel. 07071/2972958; Fax-Nr. 07071/294634). Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch den Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt.

Wir bitten um die Anmeldung von Tagungsbeiträgen. Außer Beiträgen zu den genannten Themenschwerpunkten sind auch dieses Mal wieder Kurzvorträge und Posterdemonstrationen zu weiteren Fachrichtungen der Säugetierkunde erwünscht.

Bitte melden Sie Kurzvorträge (15 min + 5 min Diskussion) sowie Posterpräsentationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer der DGS, Prof. Dr. R. Schröpfer, Fachbereich Biologie/Chemie, Barbarastr. 11, D-49069 Osnabrück (Tel. 0541/969-2847, Fax: 0541/969-2870) an. Der Anmeldung ist eine maximal einseitige Kurzfassung (Abstract, 1,5-zeilig) beizufügen. Aus ihr müssen die Fragestellung, die angewandten Methoden, die Ergebnisse und die daraus gezogenen Schlußfolgerungen ersichtlich sein. Die Kurzfassungen angenommener Beiträge werden in einem Sonderheft der Zeitschrift für Säugetierkunde publiziert. Sie sind nach folgendem Schema abzufassen: deutscher Titel, Leerzeile, englischer Titel (kleine Anfangsbuchstaben im Text; bitte ggf. einen „native speaker" konsultieren), Leerzeile, Initialen und Familienname(n) des/der Autors/Autorin bzw. der Autoren/Autorinnen in Großbuchstaben, Adresse, Leerzeile, Text (bitte **nicht** formatieren!). Aus arbeitsökonomischen Gründen bitten wir dringend darum, zusätzlich zu dieser ausgedruckten Kurzfassung möglichst noch eine fehlerfreie (!) Fassung auf Diskette (5.25" oder 3.5", IBM-kompatibler PC, DOS oder Windows) in Form eines Word- oder ASCII-Files mitzuschikken. Bitte verwenden Sie als Filebezeichnung den eigenen Namen (Initialen und Familienname, z. B. MFISCHER.TXT/DOC). Die Maße für Poster werden im Juli-Rundschreiben der DGS bekanntgegeben.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Herrn Prof. Dr. M. S. Fischer, Institut für Spezielle Zoologie und Evolutionsbiologie, Friedrich-Schiller-Universität, Erbertstr. 1, D-07743 Jena (Telefon: 03641/630301; Telefax: 03641/630392).

Redaktionelle Hinweise

Einsendung und Annahme von Manuskripten: Ms. zur Veröffentlichung sind einzusenden an den 1. Schriftleiter: Herrn Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel. e-mail: d.kruska@ifh.uni-kiel.de

Über die Annahme von Ms. zur Veröffentlichung wird gemäß Geschäftsordnung der Deutschen Gesellschaft für Säugetierkunde entschieden. Der Eingang von Ms. wird sofort bestätigt, und nach Erhalt der Gutachten werden die Autoren über die Entscheidung umgehend informiert.

Schriftwechsel, der die technische Drucklegung betrifft, ist zu richten an: Zeitschrift für Säugetierkunde, Gustav Fischer Verlag, Villengang 2, D-07745 Jena.

Äußere Form der Manuskripte: Die Ms. sind 3fach und vollständig als Original mit 2 Kopien in deutscher oder englischer Sprache einzureichen. Sie müssen mit Schreibmaschine oder als deutlich lesbare Computerausdrucke auf DIN A4-Blättern (21×29,7 cm), mit einem linken Heftrand von 4 cm und durchgehend mit einem doppelten Zeilenabstand geschrieben sein. Jedes Ms. soll auf der 1. Seite folgende Angaben enthalten: Titel der Studie; Name(n) der Autoren (männliche Vornamen nur in Initialen, weibliche ausgeschrieben); Institution(en), an der (denen) die Studie durchgeführt wurde. Ferner soll bei längeren Titeln ein kurzer Kolumnentitel (Seitenüberschrift) von maximal 72 Anschlägen angegeben werden.

Die Schrifttypen müssen einheitlich sein, ohne halbfette, gesperrte, kursive etc. Hervorhebungen. Fußnoten auf den Seiten oder Appendices am Ende sind nicht zugelassen. Autorennamen im Zusammenhang mit Literaturzitaten sind im Text mit Bleistift zu unterstreichen. Wissenschaftliche zoologische und botanische Gattungs-, Art- und Unterartnamen sind mit einer Schlangenlinie zu unterstreichen. Der Name von Erstbeschreibern bei wissenschaftlichen Namen wird nicht unterstrichen.

Im Ms. ist am Rand mit Bleistift zu vermerken, an welcher Stelle die einzelnen Abbildungen und Tabellen eingefügt werden sollen.

Am Ende der Studie, im Anschluß an das Literaturverzeichnis, sind die genauen postalischen Adressen des (der) Autoren anzugeben.

Umfang und Aufbau der Manuskripte: Manuskripte können als Originalarbeiten oder als wissenschaftliche Kurzmitteilungen veröffentlicht werden.

a) Originalarbeiten: Originalarbeiten sollen einschließlich Abbildungen, Tabellen und Literaturverzeichnis einen Gesamtumfang von 30 Ms.-Seiten nicht überschreiten. Der Text soll eine klare Gliederung aufweisen in: Abstract (in englischer Sprache), Einleitung, Material und Methode, Ergebnisse, Diskussion (oder zusammengefaßt als Ergebnisse und Diskussion), Danksagungen, Zusammenfassung und Literatur.

Bei deutschsprachigen Studien ist über dem englischen Abstract der Titel in englischer Sprache anzugeben. Bei englischsprachigen Studien ist entsprechend über der deutschen Zusammenfassung der Titel in deutscher Sprache anzugeben.

b) Wissenschaftliche Kurzmitteilungen: Wissenschaftliche Kurzmitteilungen sollen einen Gesamtumfang von 5 Ms.-Seiten nicht überschreiten. Sie enthalten kein Abstract und keine Zusammenfassung. Bei deutschsprachigen Ms. ist jedoch auf der 1. Seite zusätzlich eine englische Übersetzung des Titels anzugeben, bei englischsprachigen entsprechend eine deutsche Übersetzung. Wissenschaftliche Kurzmitteilungen sind äußerlich nicht in die Kapitel Einleitung, Material und Methode, Ergebnisse und Diskussion gegliedert, müssen aber in der textlichen Darstellung diese Strukturierung erkennen lassen.

Abbildungen: Anzahl und Größe der Abbildungen sind unbedingt auf das notwendige Mindestmaß zu beschränken. Es können nur kontrastreiche, reproduktionsfähige Originale verwendet werden, farbige Abbildungen werden nicht angenommen. Beschriftungen müssen einheitlich und wegen späterer Verkleinerung groß und kräftig sein. Auf der Rückseite sind laufende Numerierung, Zeitschrift und Autorennamen anzugeben. Alle Bildunterschriften sollen auf einem gesonderten Blatt gelistet werden.

Tabellen: Tabellen müssen auf ein Mindestmaß beschränkt werden. Jede Tabelle muß auf einem gesonderten DIN A4-Blatt angelegt sowie mit Überschrift und laufender Numerierung versehen sein. Umfangreichere Tabellen müssen auf Folgeblättern als Fortsetzung erscheinen.

Literaturverzeichnis: Jede zitierte Arbeit ist in alphabetischer Reihenfolge aufzuführen. Es soll nur international erreichbare Literatur zitiert werden. Die Zeitschriften werden mit ihrem Kurztitel angegeben.

Beispiele:

a) Zeitschriftenbeiträge:

Kalko, E. K. V; Handley, C. O. Jr. (1994): Evolution, biogeography, and description af a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá. Z. Säugetierkunde **59**, 257–273.

b) Bücher:

Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.

c) Handbuchbeiträge:

Niethammer, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

Drucklegung: Der jeweilige Hauptautor erhält sowohl die Andrucke der Bilder zur Prüfung wie auch den kompletten Umbruch seines Artikels zusammen mit dem Ms. Es dürfen nur tatsächliche Satzfehler korrigiert werden. Vom Ms. abweichende Änderungen werden dem Autor in Rechnung gestellt. Es sind die üblichen Korrekturzeichen zu verwenden. Ein als druckfertig bezeichneter Abzug ist zu senden an: Herrn Prof. Dr. Peter Langer, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität, Aulweg 123, D-35385 Giessen. e-mail: peter.langer@anatomie.med.uni-giessen.de

Sonderdrucke: Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen erhalten 50 Sonderdrucke gratis. Mehrbedarf kann gegen Berechnung bei Rücksendung des Umbruchs bestellt werden.

Publisher: Gustav Fischer Verlag GmbH & Co. KG, Branch Office Jena, P. O. Box No. 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/6 26-3; Fax ++49(0)36 41/62 65 00; e-mail: office.j@gfischer.de

Advertisement bookings: Enquiries should be directed to Gustav Fischer Verlag, Advertising Manager: Sabine Schröter, P. O. Box 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/62 64 28, Fax ++49(0)36 41/62 64 21

Advertising rates: The price list from October 1, 1994 is effective at present.

Distribution and subscription agency:

For customers **in the German speaking countries:** Please turn to your bookshop or to SFG-Servicecenter Fachverlage GmbH, Zeitschriftenvertrieb: Barbara Dressler, Villengang 2, D-07745 Jena, Germany. Phone ++49(0)36 41/62 64 44, Fax ++49(0)36 41/62 64 43;

For customers **in all other countries:** Please contact your bookshop or Stockton Press., c/o Debbie Floyd, The Subscription Dept., Houndmills, Basingstoke, Hants RG 21 6XS, UK. Phone ++44(0)12 56/5 18 98. Fax ++44/12 56/2 83 39. Subscribers in the **USA** can call toll free on ++1/800/747 3187.

Terms of delivery (1997): 1 volume consisting of 6 issues.

Subscription rate (1997): Price per volume: DM 398.00; ÖS 2 905.40; sFr 382.08; UK Sterling 183.00

Single issue price: DM 80.00; ÖS 584.00; sFr 76.80; UK Sterling 35.00

Reduced membership rates are available on request. Please turn to our publ. house.

All prices mentioned above are exclusive postage. USdollar prices are converted at the current exchange rate. We accept the following credit cards: VISA/Mastercard/American Express, (Please note card-No. and expiry date).

Banking connections:

For customers in the **German speaking countries:**

Deutsche Bank AG Jena, Konto-Nr. 6 284 707, BLZ 820 700 00.

For costumers **in the other countries:**

UK Post Office Giro Account No. 5 192 455. Full details must accompany the payment.

All prices are subject to change without notice.

Subsciption information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting, printing and binding: druckhaus köthen GmbH

Printed in Germany

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

GUSTAV FISCHER

ISSN 0044-3468
Z. Säugetierkunde
Jena · 62(1997)2 · S. 65-128
April 1997

2
1997

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **62** (1997) 65–70

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allometry of the bones of living and extinct armadillos (Xenarthra, Dasypoda)

By R. A. Fariña and S. F. Vizcaíno

Departamento de Paleontología, Universidad de la República, Montevideo, Uruguay and Departamento Paleontología Vertebrados, Universidad Nacional de La Plata, La Plata, Argentina

Abstract

This study examines the allometry of long bones in ten species of armadillo spanning the entire size range of the group, and including its five extant subfamilies. The fossil species *Propraopus grandis* (middle to late Pleistocene of South America) was included in order to assess its locomotory habits. Its mass was estimated to be about 47 kg, assuming a geometrical similarity to two species of *Dasypus*. It was concluded that the armadillos scale their humeri, ulna and partially their tibia like other digging mammals previously studied, i. e. ctenomyid rodents, but their femora as generalised mammals. The limb bone dimensions of *Propraopus grandis* are those expected for an armadillo of its size. *Priodontes maximus* was found to have a humerus stronger than expected from the general pattern of armadillos.

Introduction

Research on allometry of the leg bones has shed light on how those bones scale in relation to body mass in ungulates (McMahon 1975), bovids (Alexander 1977), mammals of varied size from shrews to elephant (Alexander et al. 1979; Biewener 1983), primates (Alexander 1985) and birds (Alexander 1983). However, the studies about mammals did not include diggers. More recently, this approach has been applied to small digging mammals, like insectivores and rodents (Bou et al. 1987) and ctemonyine rodents (Casinos et al. 1993). In those studies two hypotheses were tested and corroborated: 1) in digging mammals, the regression of the long bone length against diameter (the latter being the independent variable) involves a slope of less than 1; and 2) long bone length must scale to body mass with an exponent of less than 0.33, while the long bone diameter should do so with an exponent greater than 0.33.

Those authors mentioned the interest of undertaking this kind of study on other monophyletic groups of digging mammals. Armadillos seem to be a very suitable subject, because they are a monophyletic group of diggers, ranging in size from hundreds of grams to tens of kilograms. The fossil *Propraopus grandis* (Dasypodinae, Dasypodini), one of the giant armadillos from Middle and Late Pleistocene of South America, was included among the species considered here in order to infer its possible locomotor habits.

Material and methods

The species studied here broadly represent the systematic and size diversity of extant armadillos. They are listed below under their corresponding subfamily, following the classification proposed by Scillato-Yané (1980). Each name is followed by its collection location and number of the specimens examined. The initials MACN mean Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos

Aires, Argentina; MLP and MLP-DPV mean respectively the collections of fossils and of recent animals in the Departamento Científico de Paleontología de Vertebrados of the Museo de La Plata, Argentina; and AMNH means the American Museum of Natural History, New York, USA.
Euphrachtinae:
Chaetophractus vellerosus (MLP-DPV 74); *Chaetophractus villosus* (MLP-DPV 48); *Zaedyus pichiy* (MLP-DPV 35)
Dasypodinae:
Dasypus hybridus (MLP-DPV 65); *Dasypus novemcinctus* (MLP-DPV 80); *Dasypus kappleri* (AMNH 267011); *Propraopus grandis* (MACN 17989 and MLP 69-IX-9-9)
Tolypeutinae:
Tolypeutes matacus (MLP-DPV 13)
Priodontinae:
Priodontes maximus (MACN s/n)
Chlamyphorinae:
Chlamyphorus truncatus (MACN 471).

The masses of the specimens belonging to living species were obtained from the literature (Rood 1970; McNab 1980; Wetzel 1985).

The estimate of the mass of the fossil species *Propraopus grandis* was obtained by scaling up the specimens of *Dasypus hybridus* (MLP-DPV 65) and *Dasypus novemcinctus* (MLP-DPV s/n). These two species were chosen as models because of their close morphological and phylogenetical relationships with *Propraopus grandis* (Vizcaíno 1990).

The maximum lengths and anteroposterior diameters at or immediately below the midshaft of humeri, ulnae, tibiae and femora were measured using proper callipers in both limbs (when available) and averaged.

Using reduced major axis regression, the following regressions of log-transformed values were calculated: length against diameter, diameter against body mass, and length against body mass. The variable mentioned in the second place was in all cases the independent one.

The values of slopes for humeri and femora given by Alexander et al. (1979), who used least square regressions, were recalculated after the original data using the reduced major axis method. The other values, namely the slopes for ulna and tibia, as well as those given by Casinos et al. (1993), were directly taken from the respective paper.

Results and discussion

The masses of the studied species and the lengths and diameters of their humeri, ulna, femora and tibia are shown in table 1. The mass of *Propraopus grandis*, estimated after comparison with *Dasypus novemcinctus*, turned out to be 46.7 kg; and after *Dasypus hybridus*, 47.5 kg. Thus, we decided to use 47 kg, but our calculations or conclusions would not be altered by choosing other values within the cited range.

Table 1. Masses and long bone dimensions of the studied species of armadillos. Masses (*m*, in kg), lengths (*L*) and diameters (*D*) of humeri (*H*), ulna (*U*), femora (*F*) and tibia (*T*) in millimetres

Species	m	LH	DH	LF	DF	LC	DC	LT	DT
C. vellerosus	1.10	40.6	5.1	40.3	4.5	42.7	5.3	39.0	4.6
C. villosus	4.50	66.2	6.3	69.7	7.9	64.8	8.0	58.2	7.9
Z. pichiy	1.74	43.4	4.1	45.6	5.1	44.5	5.5	5.1	5.1
D. hybridus	2.04	48.1	4.4	69.1	7.2	53.9	6.3	53.2	7.7
D. novemcinctus	3.30	62.0	5.5	120.0	10.3	72.5	8.6	80.8	11.5
D. kappleri	10.60	80.5	14.0	17.5	12.7	94.5	11.4	91.5	16.8
P. grandis	47.00	128.0	22.0	215.0	24.9	133.0	24.3	133.8	34.8
T. matacus	1.53	41.8	4.3	62.9	5.8	51.0	6.1	57.4	4.9
P. maximus	45.19	125.0	31.5	180.0	22.3	138.3	21.0	147.8	24.5
C. truncatus	0.12	19.5	2.8	22.0	2.8	22.1	2.5	21.5	2.8

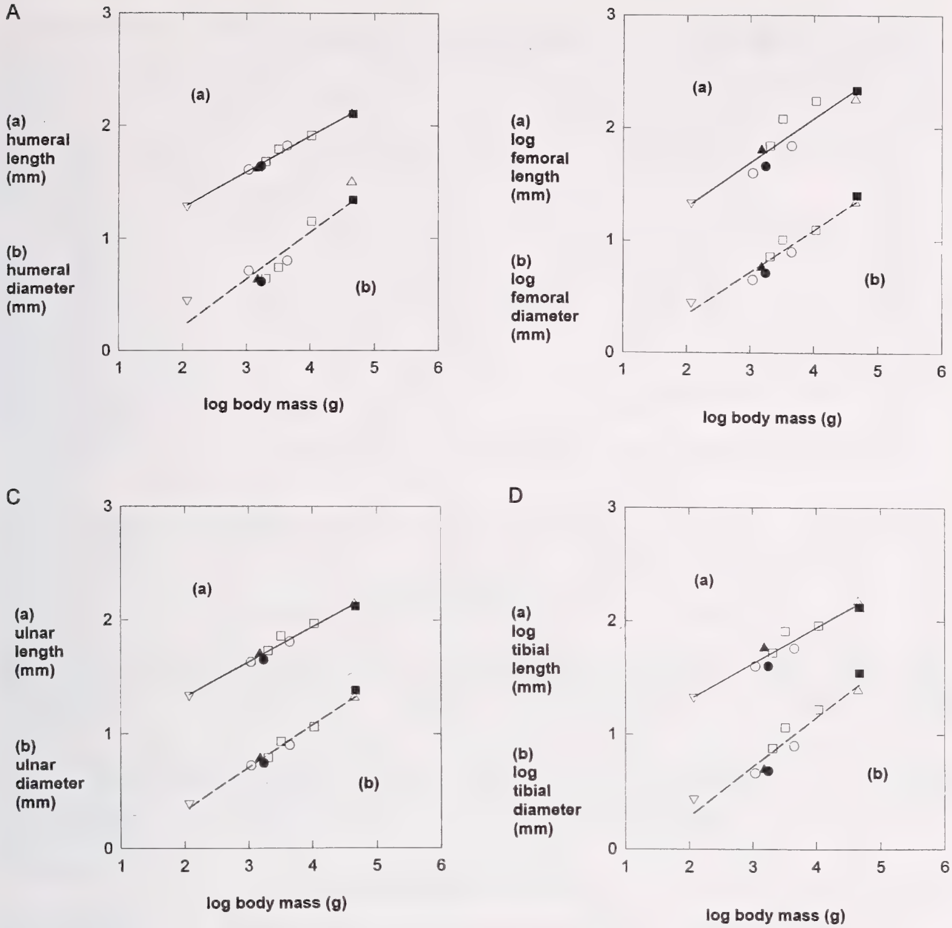


Fig. 1. Graphs on logarithmic coordinates of bone dimensions in armadillos. Linear dimensions are in millimetres and masses in grams. (A) humeral length (*a*) and diameter (*b*) against body mass; (B) ulnar length (*a*) and diameter (*b*) against body mass; (C) femur length (*a*) and diameter (*b*) against body mass; (D) tibia length (*a*) and diameter (*b*) against body mass.

Symbols:

Chaetophractus vellerosus	○	*Dasypus kappleri*	□
Chaetophractus villosus	○	*Propraopus grandis*	■
Zaedyus pichiy	●	*Tolypeutes matacus*	▲
Dasypus hybridus	□	*Priodontes maximus*	△
Dasypus novemcinctus	□	*Chlamyphorus truncatus*	▽

Our allometric curves (Fig. 1) are compared with the values recalculated after Alexander et al. (1979), and with those obtained by Casinos et al. (1993) in table 2. Since all the correlation coefficients of the calculated regressions were greater than 0.9, the differences in the values yielded by reduced major axis or least squares are very small (for further discussion, see Swartz and Biewener 1992).

In armadillos, the diameter of the humerus is related to its length by a slope of 0.70, i. e. lower than 1, as predicted by the hypothesis 1 of Bou et al. (1987). This figure is even

Table 2. Comparison of slopes of the allometric curves, after different authors. Confidence intervals shown between brackets. Abbreviations as in table 1

Slopes	Alexander et al. (1979)	Casinos et al. (1993)	this study
m/LH	0.36(0.35–0.38)	0.30(0.28–0.32)	0.32(0.31–0.33)
m/DH	0.38(0.37–0.39)	0.41(0.37–0.46)	0.45(0.39–0.51)
m/LU	0.37(0.35–0.38)	0.24(0.20–0.29)	0.31(0.30–0.33)
m/DU	0.36(0.34–0.37)	0.42(0.37–0.48)	0.38(0.36–0.39)
m/LF	0.37(0.35–0.38)	0.29(0.27–0.32)	0.41(0.36–0.46)
m/DF	0.37(0.36–0.38)	0.36(0.30–0.41)	0.39(0.36–0.42)
m/LT	0.33(0.31–0.34)	0.26(0.21–0.30)	0.33(0.30–0.36)
m/DT	0.37(0.35–0.39)	0.54(0.43–0.65)	0.45(0.41–0.50)
DH/LH	0.95(0.91–0.99)	0.75(0.67–0.84)	0.70(0.61–0.80)
DU/LU	–	0.68(0.58–0.79)	0.82(0.78–0.87)
DF/LF	0.99(0.95–1.04)	0.86(0.77–0.95)	1.07(0.98–1.16)
DT/LT	–	0.62(0.50–0.73)	0.72(0.65–0.80)

lower than the respective value obtained in ctenomyids, although the corresponding confidence intervals overlap. In the cases of the ulna and of the tibia that prediction is correct too. However, in the case of the femur the value rises to 1.07, much higher than the exponent predicted for diggers, and even higher than the recalculated figured we obtained after the data from Alexander et al. (1979). That seems to be valid also for the tibia, whose length scale in armadillos with an exponent of 0.33, the same as that yielded in the study of mammals in general, and higher than the exponent obtained in ctenomyids (0.26).

The diameters, on the other hand, scale with an exponent greater than 0.33, as predicted by the hypothesis 2 of Bou et al. (1987). Also, the humerus length behaves as predicted, i. e. with a slope of less than 0.33. However, femur length shows a slope of 0.41, much higher than the prediction of hypothesis 2 and also higher than the upper limit of the confidence interval in the results on ctenomyids of Casinos et al. (1993). This value is even higher than the average in Alexander et al. (1979) for mammals in general.

The linear dimensions of *Propraopus grandis* are approximately the expected for a generalised armadillo of its size, while *Priodontes maximus* show a thicker humerus than the average and near the prediction obtained by using the upper limit of the confidence interval of the slope.

Summing up, the humeri, ulnae and to some extent tibiae of armadillos scale in a similar way as those of digging mammals. On the other hand, their femora scale as generalised mammals and unlike the ctenomyids, the other group of digging mammals already studied. A possible explanation of this might be the wider size range of armadillos, although humeri did not seem to be affected by this factor. Another explanation might be related to the fact that, while all ctenomyids are fully subterranean, i. e. they spend most of their lives under the surface, almost all the dasypodids studied here are, to a great extent, of epigeous habits. This interpretation has the advantage of explaining the similar slope of the humeri among armadillos and ctenomyids, for in either case the excavation function of this bone is similar. Therefore, it can be stated that, from the point of view of the long bones scaling, armadillos have the forelimb of a digger and the hindlimb of a cursorial, generalised mammal.

Priodontes maximus shows much a higher value than expected for the diameter of the humerus. It must be emphasised that this is particularly important because of the fact that *Priodontes maximus* lies in the upper extreme of size range among the studied species, and, therefore, in that region of the graph the confidence limits for the regression are

wider. At the same time, the rest of its bone dimensions are the expected for its size, including those of the femur. This result is paradoxical, because this species has well-known bipedal locomotor habits (Frechkop 1949, 1950). An explanation to this observation is related to the fact that their bipedal gait (a slow walk) is not strenuous at all. Therefore, it might not pose any risk of bone failure to the hind limb. On the other hand, the humerus is involved in the much harder activities of tearing down termite nests or of excavating large galleries in hard ground.

In regard to the studied variables, the behaviour of the bone dimensions of *Propraopus grandis* is very similar to that of *Dasypus* species, with the exception of the diameter of humerus. The two smaller species of *Dasypus* show lower values for this dimension than expected for armadillos of their size, while in *Propraopus grandis* and in *Dasypus kappleri* they are in the average and slightly above, respectively. This fact suggests that the fossil species invested more in digging than these living relatives do. Unfortunately, the biology of *Dasypus kappleri* is not enough known to bolster this hypothesis more properly (Szeplaki et al. 1988).

Therefore, it can be stated that *Propraopus grandis* kept the generalised habits of the subfamily Dasypodinae, although with a body mass near 50 kg. At the same time, the sole species of armadillos attaining this size in the recent is *Priodontes maximus*, and it does it in association with a high specialisation in its trophic niche.

Acknowdledgements

We are very grateful to Prof. Robert McNeill Alexander, who kindly gave us his data on bone dimensions of mammals and commented on an earlier version of this manuscript. Also, we acknowledge Dr. Guillermo Rougier and Ms. Marta Piantanida who helped us in searching the material at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", and Dr. Ross McPhee and Dr. Wolfgang Fuchs, of the American Museum of Natural History. We also received valuable help and comments from Mr. Robert Landó, Dr. Eduardo Mizraji, Dr. Enrique P. Lessa and Dr. Gustavo Nene Pérez. Dr. Eva Danulat corrected the German in the Zusammenfassung.

Zusammenfassung

Allometrische Beziehungen von Extremitätenknochen bei lebenden und fossilien Gürteltieren (Xenarthra, Dasypoda)

Die allometrischen Beziehungen von Maßen an Extremitäten wurden bei 10 Gürteltier-Arten untersucht, einschließlich Vertretern der fünf Unterfamilien mit lebenden Arten, und in Bezug auf das gesamte Größenspektrum der Gruppe. Die fossile Art *Propraopus grandis* (Mittel- bis Oberpleistozän Südamerikas) wurde mit einbezogen, um ihre Bewegungsmöglichkeiten zu ermitteln. Aufgrund der angenommenen geometrischen Ähnlichkeit mit 2 Arten von *Dasypus* wurde die Körpermasse von *Propraopus grandis* auf etwa 47 kg geschätzt. Daraus wurde der Schluß gezogen, daß Gürteltiere ihre Oberarmknochen, Ellen und teilweise auch ihre Schienbeine wie andere grabende Säugetiere (z. B. Ctenomyide Nagetiere) ausgebildet haben, ihre Schenkelknochen jedoch entsprechend der allgemeinen Säugetiere. Die Ausmaße dieser Knochen von *Propraopus grandis* entsprechen denen eines Gürteltieres der gleichen Größe. Der Oberarmknochen von *Priodontes maximus* ist stärker ausgebildet als der der übrigen Gürteltiere.

References

Alexander, R. McN. (1977): Allometry of the limb bones of antelopes (Bovidae). J. Zool. (London) **183**, 125–146.

Alexander, R. McN. (1983): Allometry of the bones of moas (Dinornithes) and other birds. J. Zool. (London) **200**, 215–231.

Alexander, R. McN. (1985): Body size and limb design in Primates and other mammals. In: Size and scaling in Primate biology. Ed. by W. L. Jungers. New York: Plenum Press. Pp. 337–343.

Alexander, R. McN.; Jayes, A. S.; Maloiy, G. M. O.; Wathuta, E. M. (1979): Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). J. Zool. (London) **189**, 305–314.

Biewener, A. A. (1983): Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. J. Exp. Biol. **105**, 147–171.

Bou, J.; Casinos, A.; Ocaña, J. (1987): Allometry of the limb bones of insectivores and rodents. J. Morph. **192**, 113–123.

Casinos, A.; Quintana, C.; Viladiu, C. (1993): Allometry and adaptation in the long bones of a digging group of rodents (Ctenomyinae). Zool. J. Linn. Soc. **107**, 107–115.

Frechkop, S. (1949): Notes sur les Mammifères XXXVI. Explication biologique, fournie par les tatous, d'un des caractères distinctifs analogues chez les pangolis. Bull. Inst. Roy. Sc. Nat. Belgique **25**, 1–12.

Frechkop, S. (1950): La locomotion et la structure des tatous et des pangolins. An. Soc. Roy. Zool. Belgique **80**, 5–8.

McMahon, T. A. (1975): Allometry and biomechanics: limb bones in adult ungulates. Am. Nat. **109**, 547–563.

McNab, B. K. (1980): The physiological signification of body size. J. Mammalogy **61**, 606–627.

Rood, J. P. (1970): Notes on the behaviour of the pigmy armadillo. J. Mammalogy **51**, 179.

Scillato-Yané, G. J. (1980): Catálogo de los Dasypodidae fósiles (Mammalia, Edentata) de la República Argentina. Actas II Congr. Arg. Pal. Bioestr. y I Congr. Lat. Paleont. **3**, 7–36.

Szeplaki, E.; Ochoa, J.; Clavijo, A. (1988): Stomach contents of the greater long-nosed armadillo (*Dasypus kappleri*) in Venezuela. Mammalia **52**, 422–425.

Swartz, S. M.; Biewener, A. A. (1992): Shape and scaling. In: Biomechanics (Structures and Systems): a practical approach. Ed. by A. A. Biewener. Oxford: Oxford Univ. Press. Pp. 21–43.

Vizcaíno, S. F. (1990): Sistemática y evolución de los Dasypodinae Bonaparte, 1838 (Mammalia, Dasypodidae). Unpubl. PhD Dissertation, Universidad de La Plata.

Wetzel, R. H. (1985): Taxonomy and distribution of armadillos, Dasypodidae. In: Evolution and ecology of armadillos, sloths and vermilingua. Ed. by G. G. Montgomery. Washington, London: Smithsonian Institution Press. Pp. 23–46.

Authors' addresses: R. A. Fariña, Departamento de Paleontología, Facultad de Ciencias, Tristán Narvaja 1674, 11200 Montevideo, Uruguay and S. F. Vizcaíno, Departamento Paleontología Vertebrados, Universidad de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina

Z. Säugetierkunde **62** (1997) 71–85

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Gebißanomalien bei nordatlantischen Phociden (Mammalia, Phocidae)

Von S. Könemann und P. J. H. van Bree

Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam, Nederland

Eingang des Ms. 09. 05. 1996
Annahme des Ms. 26. 10. 1996

Abstract

Aberrant dentitions in North Atlantic phocids (Mammalia Phocidae)

In order to compare aberrant dentitons in North Atlantic phocids, complete skulls and mandibles of 1006 specimens were examined. Among these were 305 harbour seals (*Phoca vitulina*), 31 ringed seals (*Phoca hispida*), 73 harp seals (*Phoca groenlandica*), 54 grey seals (*Halichoerus grypus*), 17 bearded seals (*Erignathus barbatus*), and 526 hooded seals (*Cystophora cristata*). For both sexes anomalies of different types were described in six categories: teeth in abnormal locations and/or positions, supernumerary teeth, 'true' absent teeth, form variations of teeth, and (apart from these) rare or exceptional dental anomalies. Because the Amsterdam collection of hooded seals mainly consisted of single mandibles (409), the frequencies of aberrations were calculated per individuals as well as per jaw quadrants. Total frequencies (anomalies of all categories per quadrants) occurred in 1.6% (*P. vitulina*), 5.6% (*P. hispida*), 6.6% (*P. groenlandica*), 8.3% (*H. grypus*), 11.8% (*E. barbatus*), and 13.2% (*C. cristata*) of all specimens respectively. These remarkable interspecific differences were accompanied by varying percentages in the single categories, so that each species showed an own, characteristical pattern of anomalies with regard to the topography and numbers of the tooth aberrations concerned.

Einleitung

Gebißanomalien bei Säugetieren gelten als normal, solange sie die Grenzwerte der jeweils arttypischen Abweichungshäufigkeiten nicht überschreiten. Zu den markantesten Abweichungen einer Zahnformel gehören überzählige Zähne (Hyperdention oder Polydontie), fehlende Zähne (Oligodontie), sowie Zähne in abnormen Stellungen oder Lagen (Stellungs- und Positionsanomalien).

Colyer (1936) fand in acht Fissipedia-Familien (N = 7162) einen durchschnittlichen Anteil überzähliger Zähne in 1,8% aller Fälle; Stellungsanomalien erreichten Werte von gemittelt 15,0%. In einer Mauswiesel-Population (*Mustela nivalis*) wurden bei 93 untersuchten Tieren sowohl poly- und oligodonte Gebisse (jeweils 6,5%) als auch Zähne in abnormen Stellungen (4,3%) und Positionen (6,5%) nachgewiesen (Neuenschwander und Lüps 1975).

Van Bree und Sinkeldam (1969) beschrieben Oligodontie bei westeuropäischen Füchsen (*Vulpes vulpes*) als den am häufigsten vertretenen Anomalietypus: von 293 examinierten Schädeln besaßen 2,8% Gebisse mit fehlenden Zähnen, wobei der M_3 mit 10,9% die höchste Frequenz erzielte.

Oft liegt bei vergleichenden Untersuchungen von Carnivoren der prozentuale Anteil von Zahn- und Gebißanomalien bei Pinnipediern vergleichsweise hoch: Colyer (1936)

gab das Vorkommen überzähliger Zähne bei Otariiden mit 5,0% und mit 7,9% bei Phociden an. Bateson (1892) beschrieb für die gleichen Gruppen polydonte Gebisse in 4,0% und 7,3% aller Fälle.

Erstaunlich für Robben ist die interspezifische Variation von Abweichungstypen und -häufigkeiten. Diese Thematik ist bisher selten in Veröffentlichungen behandelt worden. Suzuki et al. (1990) verglichen numerische Anomalien bei drei Robbenarten und fanden auffällige interspezifische Schwankungen: Der Anteil überzähliger Zähne lag zwischen 6,0% (*Phoca largha*) und 11,8% (*Phoca fasciata*), fehlende Zähne erreichten Häufigkeiten von 0,9% (*Phoca largha*) und 11,8% (*Phoca fasciata*).

Das Auftreten von Dentitionsanomalien gilt als gewöhnlich für Bart- und Ringelrobben (Stewart und Stewart 1987 a). Bei Seehunden (*Phoca vitulina*) werden Abweichungen weniger häufig wahrgenommen. Bis dato sind keine Gründe für derartig starke Schwankungen innerhalb phylogenetisch eng verwandter Pinnipediergruppen bekannt.

In dieser Studie sollen bei sechs Robbenarten Anomalien und Besonderheiten des Gebisses untersucht werden. Um einen interspezifischen Vergleich zu ermöglichen, sollen die Abweichungen, nach Kategorien getrennt, qualitativ und quantitativ beschrieben werden.

Material und Methode

Insgesamt wurden 1 006 Individuen sechs nordatlantischer Phocidenarten untersucht. Hierfür standen die Sammlungen der folgenden Institute zur Verfügung: das ‚Zoölogisch Museum Amsterdam' (ZMA), das ‚Nationaal Natuurhistorisch Museum' in Leiden (RMNH) und das ‚Natuur Museum' in Rotterdam (NMR).

Unter den examinierten Schädeln befanden sich 17 Bartrobben (*Erignathus barbatus* (Erxleben, 1777)), 31 Ringelrobben (*Phoca hispida* Schreber, 1775), 54 Kegelrobben (*Halichoerus grypus* (Fabricius, 1791)), 73 Sattelrobben (*Phoca groenlandica* Erxleben, 1777), 305 Seehunde (*Phoca vitulina* Linnaeus, 1758) und 526 Klappmützen (*Cystophora cristata* (Erxleben, 1777)). Von den Ringelrobben gehörten sechs Exemplare verschiedenen Unterarten an: *P. h. ochotensis* Pallas, 1811 (3), *P. h. saimensis* Nordquist, 1899 (1) und *P. h. botnica* Gmelin, 1785 (2). Diese Tiere wurden statistisch nicht gesondert erfaßt.

Die Exemplare wurden auf Stellungs- und Positionsanomalien, auf Abweichungen der Zahnform, auf überzählige Zähne und auf ‚echte' Oligodontie (alle fehlenden Zähne, die nicht traumatisch oder altersbedingt verloren wurden) untersucht (Tab. 1). Überzählige Zähne wiesen gelegentlich auch Abweichungen der Form (Reduzierung) und/oder der Postion auf. In diesen Fällen wurde lediglich die Überzähligkeit als Abweichung erfaßt.

Neben solchen markanten Anomalien traten in unterschiedlichem Maße Variationen auf, die nur geringfügige Abweichungen vom Normgebiß darstellten und aus diesem Grund statistisch nicht mitberücksichtigt worden sind. Kennzeichnend für diese (meist artspezifischen) Variationen ist ein allmählicher Übergang zwischen Norm und Extrem, wie zum Beispiel die variierende Anzahl der Postcanini-Höcker bei Sattelrobben. Solche Formvariationen werden im folgenden als ‚Trends' bezeichnet (siehe auch Burns und Fay 1970).

Die Sammlungen enthielten überwiegend vollständige Crania. Eine Ausnahme stellte die Amsterdammer Klappmützen-Sammlung dar, die überwiegend aus einzelnen Mandibeln bestand (409 von 526 Individuen). Da das Auftreten von Anomalien jedoch oft einer symmetrischen Verteilung von betroffenen Isomeren in beiden Mandibeln- und/oder Maxillarenhälften entspricht, ist die Anzahl der Abweichungen von *C. cristata*, verglichen mit Individuen, die vollständige Gebisse besitzen, unterrepräsentiert. Aus diesem Grund wurden neben den Abweichungshäufigkeiten pro Individuen auch die Anomalien pro Kieferquadranten ermittelt (Tab. 2).

Generell wurden bei Schädeln mit unvollständigen Gebissen die vorhandenen Zähne beschrieben und in die Berechnung miteinbezogen. Hierbei entspricht jedes examinierte Exemplar einem Individuum, bzw., je nach Vollständigket, einem bis vier Quadranten. Das Auftreten von Anomalien in linken und rechten Kieferhälften wurde als gleichverteilt vorausgesetzt (Lüps 1990; Stewart und Stewart 1987 a).

Tabelle 1. Anzahl der Topographie der Gebißanomalien bei sechs untersuchten Robben-Arten. PC = Postcaninus, C = Caninus, I = Incisivus, OK = Oberkiefer, UK = Unterkiefer, n. b. = Geschlecht nicht bekannt, N (in Klammern) = Anzahl Individuen. [1] = Wurzeln liegen buccal frei, [2] = Hypoplasie.

Spezies/Geschlecht			Überzählige Zähne			Fehlende Zähne			Form-anomalien			Positions-anomalien			Stellungs-anomalien			Sonstige Anomalien		
			PC	C	I	PC	C	I	PC	C	I	PC	C	I	PC	C	I	PC	C	I
Phoca vitulina [N = 305]	♀♀	OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[144]	UK	–	–	–	3	–	1	–	–	2	–	–	–	–	–	–	–	–	–
	♂♂	OK	3	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
	[94]	UK	1	–	–	5	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	n. b.	OK	–	–	–	–	–	–	2	1	–	–	–	–	–	–	–	–	–	–
	[67]	UK	1	–	–	1	–	–	1	1	4	–	–	–	–	–	–	–	–	–
Phoca hispida [N = 34]	♀♀	OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[5]	UK	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	♂♂	OK	–	–	–	4	–	–	–	2	–	–	–	–	–	–	–	–	–	–
	[8]	UK	–	–	–	2	–	–	–	–	–	–	–	1	–	–	–	–	–	–
	n. b.	OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[21]	UK	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Phoca groenlandica [N = 73]	♀♀	OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4[1]	–	–
	[30]	UK	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–
	♂♂	OK	2	–	–	–	–	–	2	–	–	2	–	–	2	–	–	5[1]	–	–
	[25]	UK	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	n. b.	OK	1	–	–	–	–	–	3	–	–	–	–	–	–	–	–	–	–	–
	[18]	UK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Erignathus barbatus [N = 17]	♀♀	OK	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[3]	UK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	♂♂	OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[2]	UK	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	n. b.	OK	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[12]	UK	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–
Halichoerus grypus [N = 54]	♀♀	OK	2	–	–	–	–	–	–	–	1	–	–	–	1	–	–	–	–	–
	[17]	UK	–	–	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–
	♂♂	OK	–	–	–	–	–	–	–	–	2	4	–	–	6	–	–	–	–	–
	[30]	UK	–	–	–	–	–	–	1	–	–	1	–	–	2	–	–	–	–	–
	n. b.	OK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[7]	UK	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cystophora cristata [N = 526]	♀♀	OK	3	–	–	3	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[305]	UK	23	–	1	11	–	–	20	–	–	–	–	–	–	–	–	1[2]	–	–
	♂♂	OK	6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[205]	UK	13	–	2	5	–	–	7	–	1	1	–	1	–	–	–	–	–	–
	n. b.	OK	–	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	[16]	UK	–	–	–	4	–	–	1	–	–	–	–	–	–	–	–	–	–	–

Tabelle 2. Prozentuale Anteile der verschiedenen Anomalien, jeweils bezogen auf betroffene Individuen (links) und betroffene Quadranten (rechts). Bei *Cystophora cristata* wurden Stellungsanomalien nicht anzahlmäßig erfaßt, sondern lediglich als Trend beschrieben. % total = Anteil der insgesamt betroffenen Individuen (Quadranten), PoD = Polydontie, OiD = Oligodontie, FoA = Formanomalie, PsA = Positionsanomalie, StA = Stellungsanomalie, Son. = Sonstige Anomalien. [1] = Wurzeln liegen buccal frei, [2] = Hypoplasie.

Spezies/Geschlecht		Individuen										Quadranten									
		N	N	% PoD	% OiD	% FoA	% PsA	% StA	% Son.	% total	% total	N	N	% PoD	% OiD	% FoA	% PsA	% StA	% Son.	% total	% total
	♀♀		144	0,0	1,4	0,7	0,0	0,0	0,0	2,1			542	0,0	0,7	0,2	0,0	0,0	0,0	0,9	
Phoca vitulina	♂♂	305	94	2,1	2,1	1,1	0,0	0,0	0,0	5,3	3,9	1 142	347	0,9	1,2	0,3	0,0	0,0	0,0	2,3	1,6
	n. b.		67	1,5	1,5	3,0	0,0	0,0	0,0	6,0			253	0,4	0,4	1,2	0,0	0,0	0,0	2,0	
	♀♀		5	0,0	20,0	0,0	0,0	0,0	0,0	20,0			20	0,0	5,0	0,0	0,0	0,0	0,0	5,0	
Phoca hispida	♂♂	34	8	0,0	25,0	12,5	12,5	0,0	0,0	37,5	14,7	126	28	0,0	14,3	3,6	3,6	0,0	0,0	17,9	**5,6**
	n. b.		21	0,0	4,8	0,0	0,0	0,0	0,0	4,8			78	0,0	1,3	0,0	0,0	0,0	0,0	1,3	
	♀♀		30	0,0	0,0	3,3	0,0	0,0	6,7[1]	10,0			119	0,0	0,0	0,8	0,0	0,0	2,5[1]	3,4	
Phoca groenlandica	♂♂	73	25	8,0	0,0	4,0	4,0	4,0	8,0[1]	24,0	16,4	289	100	3,0	0,0	2,0	2,0	2,0	4,0[1]	11,0	6,6
	n. b.		18	5,6	0,0	11,1	0,0	0,0	0,0	16,7			70	1,4	0,0	4,3	0,0	0,0	0,0	5,7	
	♀♀		3	33,3	0,0	0,0	0,0	0,0	0,0	33,3			12	16,7	0,0	0,0	0,0	0,0	0,0	16,7	
Erignathus barbatus	♂♂	17	2	50,0	0,0	0,0	0,0	0,0	0,0	50,0	29,4	68	8	12,5	0,0	0,0	0,0	0,0	0,0	12,5	11,8
	n. b.		12	16,7	0,0	8,3	0,0	0,0	0,0	25,0			48	6,3	0,0	4,2	0,0	0,0	0,0	10,4	
	♀♀		17	5,9	0,0	5,9	5,9	5,9	0,0	17,6			68	2,9	0,0	1,5	1,5	1,5	0,0	7,4	
Halichoerus grypus	♂♂	54	30	0,0	0,0	6,7	6,7	6,7	0,0	20,0	16,7	216	120	0,0	0,0	2,5	4,2	4,2	0,0	10,8	8,3
	n. b.		7	0,0	0,0	0,0	0,0	0,0	0,0	0,0			28	0,0	0,0	0,0	0,0	0,0	0,0	0,0	
	♀♀		305	7,9	3,9	4,3	0,0	–	0,3[2]	14,8			354	7,3	4,0	3,7	0,0	–	0,3[2]	13,8	
Cystophora cristata	♂♂	526	205	7,8	2,4	4,4	1,0	–	0,0	13,7	14,4	652	270	6,7	1,9	3,0	0,7	–	0,0	11,5	13,2
	n. b.		16	0,0	18,8	6,3	0,0	–	0,0	18,8			28	0,0	21,4	3,6	0,0	–	0,0	21,4	

Aufgrund der ausgeprägten Homodontie bei Pinnipediern soll auf die Differenzierung der Backenzähne in Prämolaren (PM1–4) und Molaren (M1) zugunsten der Einteilung in Postcanini (PC1–5) verzichtet werden. Die Dimensionen eines Zahnes werden wie folgt beschrieben: Höhe = Abmessung von der Kronenspitze bis zum Alveolarrand; Länge = größte Abmessung anteroposteriad; Breite = größte Abmessung buccolinguad.

Ergebnisse

Phoca vitulina

Zahnformel: $I^3{}_2\ C^1{}_1\ PC^5{}_5 = 34$. PC2–5 mit zwei Wurzeln, sonst alle Zähne mit einfacher Wurzel. Trends: Die Zähne standen, vor allem bei juvenilen und subadulten Tieren, eng aufeinander, was eine mehr oder weniger starke transversale Schrägstellung der PC (meist PC2–4) verursachte. Die PC-Reihen des Oberkiefers (OK) liefen aufgrund der engen Stellung posteroanteriad nach innen, so daß die PC^1 linguad dicht auf den Canini lagen. Als weitere Folge der Enge schienen die Incisiven des Unterkiefers (UK) mehr übereinander (dorsoventral) als nebeneinander zu stehen. Die besonderen Stellungs- und Positionsmerkmale der PC ergaben eine beinahe lückenlose Okklusion. Bei adulten Individuen konnten oft einseitige Abnutzungserscheinungen der PC-Nebenhöcker beobachtet werden, die durch die apikalen Zacken des Opponenten verursacht worden waren.

Anomalien: Es wurden überzählige Zähne, fehlende Zähne und Formanomalien von Zähnen festgestellt. Positions- und Stellungsanomalien kamen (außer bei überzähligen Zähnen) nicht vor. Auffällig war, daß keiner der 144 weiblichen Schädel ein polydontes

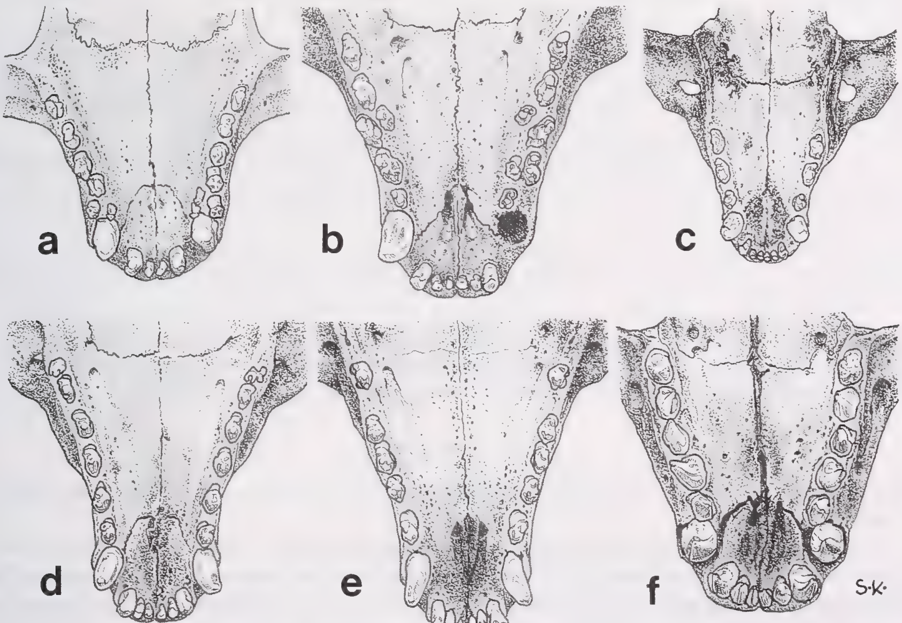


Abb 1. a: 3 überzählige, leicht reduzierte PC^1 bei *Cystophora cristata* (ZMA 18060); b: 3 überzählige PC bei *Phoca vitulina* (ZMA 23724); c: beidseitig abwesende PC^{4-5} bei *Phoca h. hispida* (ZMA 17184); d: *Phoca groenlandica* (ZMA 20333) mit 2 überzähligen PC in Position PC^6; e: Positionsanomalie (PC^5 extrem distal) und Stellungsanomalie (PC^1 anteroposteriad geneigt) bei *Phoca groenlandica* (ZMA 20410); f: *Halichoerus grypus* (ZMA 5851) mit Stellungsanomalie (PC^2 buccad verdreht).

Gebiß aufwies. Polydontie trat ausschließlich in Form nicht-reduzierter PC auf, die, lingual oder buccal, außerhalb der normalen Zahnreihe im Bereich der PC2–4 wuchsen (Abb. 1 b). Ihre Anzahl pro Gebiß variierte von einem bis 3 PC.

Von Oligodontie betroffen waren 9 Mandibeln, in denen 8 PC_1, 1 PC_2 und 1 Incisivus nicht ausgebildet waren.

Formanomalien konnten bei allen Zahntypen festgestellt werden: I_{1-2} in Längsrichtung miteinander verwachsen (ZMA 24928); linker I_{1-2} etwa 1,8mal größer als rechter I_{1-2} (ZMA 19648); PC^1 vergrößert, ähnelt Caninus (ZMA 12647). Die auffälligste Formabweichung eines adulten Individuums unbekannten Geschlechts (RMNH, Cat. Jentink p. 120 d) bestand aus insgesamt acht Zähnen, die als nicht rekonstruierbare Bruchstücke in Scherben- und Nadelform aus den Zahnreihen ragten (OK links: PC^{1-2}, C^1; UK links: PC_{1-2}, C_1, I_{1-2}). Maxillare und Mandibel waren auf dieser linken Seite stark erodiert und verformt, die I^{1-2} und der PC^3 fehlten (keine Absenz). Der unzersplitterte PC_3 der linken Kieferhälfte war, möglicherweise aufgrund der Absenz eines Antagonisten, abnorm erhöht. Es konnte nicht ausgeschlossen werden, daß diese untypische Abweichung traumatischen Ursprungs war. Hierfür sprach vor allem, daß zwei gleichgroße, opponierende Bereiche von OK und UK betroffen waren. Ein derartiges Trauma könnte zum Beispiel durch einen kräftigen Biß auf einen harten Gegenstand entstanden sein. Die Tatsache, daß die einzelnen Bruchstücke ‚wie gewachsen' nebeneinanderstanden, lieferte jedoch einen begründeten Hinweis für eine angeborene Abweichung. Bei einer Verletzung wäre eher der Verlust der Abbrüche und ein persisterendes Kernstück zu erwarten gewesen.

Phoca hispida

Zahnformel: $I^3{}_2\ C^1{}_1\ PC^5{}_5 = 34$. I, C und PC1 mit einfacher Wurzel, PC2–5 mit zwei Wurzeln.

Trends: Die Nebenhöcker der PC2–5 waren, verglichen mit *P. vitulina*, relativ lang und spitz. Ihre Anzahl (2 bis 4) variierte ebenso auffällig wie ihre Position auf der Krone, so daß sich als Extremfälle 1 zweizackiger PC mit mesialem apikalen Höcker und 1 PC mit drei lateralen und einem zentralen apikalen Höcker gegenüberstanden.

Anomalien: Bei den examinierten Ringelrobben konnten in keinem Fall überzählige Zähne festgestellt werden. Die häufigste Abweichung bestand aus 9 fehlenden PC in beiden Kiefern bei *P. h. hispida*. Jeweils betroffen waren: 1 PC_1 und die PC^{4-5} in beiden Kieferhälften bei einem juvenilen ♀ (ZMA 17184, Abb. 1 c); die PC_{4-5} der linken Seite (ZMA 24384, ♀); de PC_5 auf beiden Seiten bei 2 Individuen (ZMA 24926, ♂; RMNH, Cat. Jentink 1887). Ebenfalls bei *P. h. hispida* wurde eine Lageanomalie des rechten I_1 gefunden, der dorsal über dem I_2 stand (siehe auch Lönnberg 1922; Wyss 1994; Burns und Fay 1970). Eine 1995 in Spanien (!) gestrandete Ringelrobbe (ZMA 25003, vermutlich *P. h. botnica*) besaß zwei C^1, die apikal gespalten waren (Abb. 2 a).

Phoca groenlandica

Zahnformel: $I^3{}_2\ C^1{}_1\ PC^5{}_5 = 34$. PC2–5 mit zwei Wurzeln, alle übrigen Zähne mit einfacher Wurzel.

Trends: Wie bei *P. hispida* variierten Anzahl und Form der Nebenhöcker bei den PC2–5. Es war schwierig zu entscheiden, welche Formvariante die Norm darstellte: zweizackige PC (apikaler Höcker mit einem Nebenhöcker) schienen ebenso häufig vorzukommen wie dreizackige. In einigen wenigen Fällen wurden vierzackige PC gefunden.

Anders als bei *P. vitulina* standen die PC weiträumiger, mit kleinen Zwischenabständen – die Kiefer waren verhältnismäßig langgestreckt. Hierdurch ergab sich eine Okklusion mit entsprechend größeren Lücken. Die Zahnreihen der Maxillaren waren schmaler und stärker aufgefaltet als bei den beiden anderen untersuchten *Phoca*-Arten. Ein weiteres Charakteristikum des Gebisses waren die kräftig entwickelten I^3.

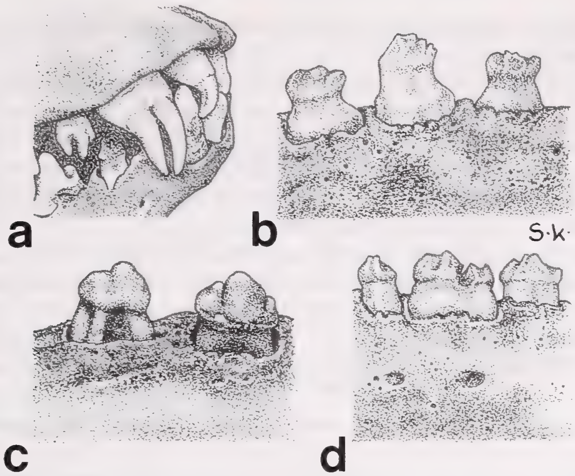


Abb. 2. a: Gespaltener C^1 (vermutlich *Phoca h. botnica*, ZMA 25003); b: Verdickung der Wurzeln und Kronenvariation bei *Cystophora cristata* (beides mäßig ausgeprägt und nicht als Abweichungen registriert); c: PC^5 mit dreifacher Wurzel bei *Phoca groenlandica* (ZMA 19491); d: Formanomalie des PC_2 bei *Cystophora cristata* (ZMA 18109/200).

Anomalien: Keines der examinierten Gebisse hatte fehlende Zähne. Ansonsten konnten Abweichungen aller Kategorien festgestellt werden, die jedoch geschlechtsspezifisch ungleich verteilt waren. Der leicht erhöhte PC_1 eines ♀ (ZMA 20299) hatte einen mesialen apikalen Höcker mit 3 deutlich entwickelten Nebenzacken, die eine Vergrößerung des Kronenbereichs bewirkten. Ebenfalls vierzackig bei ansonsten normaler Form und Größe waren die PC_1 eines ♂ (ZMA 20412). Im OK desselben Individuums fanden sich zwei abnorm große dreizackige PC^1. In einem weiteren Fall (RMNH, Cat. g) wurde ein vergrößerter vierzackiger PC^1 gefunden. Bei einem Exemplar unbekannten Geschlechts wurden als Formvariationen zwei PC^5 mit einer dritten Wurzel festgestellt (ZMA 19491). Diese zusätzliche Wurzel war über ihre gesamte Längsachse mit der Nachbarwurzel verwachsen (Abb. 2 c).

Polydontie betraf insgesamt 4 PC, die in drei Fällen als reduzierte PC6 den Verlauf der Zahnreihe fortsetzten (Abb. 1 d). Als Einzelfall (ZMA 20334, ♂) trat ein doppelt angelegter PC_1 auf.

Neben solchen allgemein vorkommenden Abweichungen lagen bei vier Maxillaria die PC zum Teil buccal im Wurzelbereich frei. Diese offenen Alveolen kamen in drei Fällen beidseitig vor (ZMA 20366, 20408 und 25004). Betroffen waren aussschließlich die distalen PC des OK (PC^{4-5} oder PC^5).

Erignathus barbatus

Zahnformel: $I^3{}_2$ $C^1{}_1$ $PC^5{}_5 = 34$. Wurzeln wie bei den *Phoca*-Arten.

Trends: Die untersuchten Bartrobben besaßen auffällig kleine Canini. Die PC standen weiträumig in den Zahnreihen, wodurch sich eine lückenhafte Okkluson ergab. Durch die lockere Verwurzelung in den Alveolen war in 7 von 17 Fällen mehr als die Hälfte aller 34 Zähne verlorengegangen. Alle sieben Schädel stammten von adulten Tieren mit Condylobasal-Längen zwischen 21,5 und 22,4 cm. Zwei Individuen hatten ihr komplettes Gebiß verloren. Die Kiefer adulter Tiere zeigten oft altersbedingte Auflösungserscheinungen (Osteoporose), die den außergewöhnlich häufigen Zahnverlust zu fördern schienen (siehe auch King 1991). Gegenüber den drei *Phoca*-Arten war die Abnutzung der Zähne extre-

mer ausgeprägt: bei drei Individuen waren alle vorhandenen Zähne bis auf rudimentäre Stummel abgenutzt.

Anomalien: 4 Individuen hatten überzählige Zähne (5 PC im OK, 1 I im UK). In zwei Fällen war aufgrund der starken Abnutzungserscheinungen keine Rekonstruktion der Zahntypen oder -formen möglich. Alle überzähligen PC waren in den Verlauf der Zahnreihe integriert. Der überzählige linke PC^3 eines ♀ stand bei unverminderter Größe schräg zur Kieferlängsrichtung (ZMA 20343). Ein ♂ besaß einen überzähligen Incisivus dorsal über dem rechten I_1 stehend (ZMA 24695).

Es wurde nur eine einzelne Formabweichung bei einem adulten Tier unbekannten Geschlechts gefunden (RMNH, Cat. a): hier waren beide C_1 abnorm klein mit einer kronenähnlichen Verdickung im okklusalen Bereich.

Halichoerus grypus

Zahnformel: $I^3{}_2$ $C^1{}_1$ $PC^5{}_5 = 34$. PC5 mit zwei Wurzeln, alle übrigen Zähne mit einfachen Wurzeln.

Trends: Alle Zähne waren vergleichsweise groß und kräftig entwickelt. Die Nebenhökker der okklusal spitz zulaufenden PC waren in der Regel stark bis völlig reduziert. Diese Reduktion betraf die Mandibeln in geringerem Maße als die Maxillaria: besonders bei den PC_{4-5} wurden oft kleine, aber deutlich entwickelte laterale Zacken festgestellt. Bedingt durch die Reduzierung der Nebenhöcker tendieren Kegelrobben stärker als die übrigen hier beschriebenen Arten zu einem homodonten Gebiß. In diesen Trend paßte auch die bemerkenswerte Größe der OK-Incisiven, insbesondere der I^3, die unwesentlich kleiner als die benachbarten Canini waren.

Trotz der langgestreckten Kiefer wuchsen die Zähne in dichter Staffelung. Ausgenommen hiervon war der PC^5, der häufig distal relativ distanziert zu finden war. Die 4 UK-Incisiven standen aufgrund der engen Stellung tendenziell eher (dorsoventral) übereinander als nebeneinander. Offensichtlich wurde die räumliche Enge u. a. durch die voluminösen Wurzeln der PC bewirkt. Die einfachen Wurzeln der PC1–4 schienen jeweils aus einer verwachsenen, ursprünglich doppelten Wurzel entstanden zu sein. Diese Vermutung ließ sich durch die Tatsache stützen, daß die Wurzeln longitudinal eine nahtartige Furche aufwiesen, die vor allem bei den PC3–4 deutlich entwickelt war.

Anomalien: Es konnten bei 54 Exemplaren keine fehlenden Zähne festgestellt werden. Polydontie trat nur in einem Fall auf: ein neugeborenes ♀ besaß stummelartig reduzierte PC^6 im regulären Verlauf der Zahnreihen (ZMA 20733). Bei drei Individuen wurden die folgenden Formanomalien gefunden: ein abnorm vergrößerter I^3 (ZMA 14293, ♂); ein adultes ♂ (NMR ohne Nr.) mit reduziertem I^2 (Höhe: 3 mm) und abnorm vergrößertem PC_3 (beide links bei ansonsten extrem geschwollenem UK); ein juveniles ♀ (ZMA 19292) mit einem I^2, der im okklusalen Bereich die Anlage eines Höckers erkennen ließ (bei ansonsten pathologisch erodierten Kiefern).

Bemerkenswert häufig wurden Stellungs- und Positionsanomalien konstatiert. In allen Fällen schienen die Abweichungen auf die enge Zahnstellung zurückzuführen zu sein. Zähne in abnormen Stellungen waren ausschließlich PC (9), die durch die gegenseitige räumliche Behinderung zu einer Drehung in ihren Alveolen gezwungen worden waren. Diese PC standen entweder, im Falle der PC_4, quer zur Längsrichtung der Zahnreihe (beide PC_4 bei ZMA 10905) oder, bei den PC^{1-2}, gegeneinander versetzt (ZMA 2744, 5851 und 10905; Abb. 1 f), so daß ihre Kronenspitzen entweder zur buccalen oder zur lingualen Seite geneigt waren (normalerweise waren die Spitzen der leicht gekrümmten PC linguad gerichtet).

Zu den Positionsanomalien gehörten ein I_2, der ventral unter dem benachbarten I_1 stand (ZMA 5851), sowie 5 PC, die buccal (1 PC^2) oder lingual (4 PC1) außerhalb der Zahnreihe wuchsen (ZMA 15986; NMR ohne Nr.). Die Gebisse einiger adulter Tiere

zeigten außergewöhnliche, einseitige Verschleißerscheinungen: bei relativ gut erhaltenen PC waren die Incisiven bis auf das Zahnfleisch abgenutzt. Die Incisiven des OK waren hiervon relativ stärker betroffen.

Cystophora cristata

Zahnformel: $I^2{}_1$ $C^1{}_1$ $PC^5{}_5 = 30$. Alle Zähne mit einfacher Wurzel.

Trends: Die Crania der examinierten Klappmützenschädel besaßen als charakteristisches Merkmal unterproportional verkürzte Schnauzen. In den Mandibeln betrug die Länge der Zahnreihen nur etwa $^2/_3$ der dorsalen (horizontalen) Kieferlänge, wodurch das Gebiß rostrad verschoben wirkte. Einzelne PC der Mandibeln standen häufig quer zur Kieferlängsrichtung. Die beiden Incisivi des UK waren vergleichsweise klein und verkümmert. Im Gegensatz dazu wirkten die I^2 des OK, die beinahe die Größe der Canini erreichten, wie Zähne eines anderen Typus.

Die Morphologie der PC wurde durch flache, distinkt geformte Kronen bestimmt, die unterschiedlich hoch und/oder breit entwickelt sein konnten (Abb. 2 b). Apikale und laterale Höcker waren mehr oder weniger stark reduziert – die Kronen wiesen in vielen Fällen eine radial verlaufende Furchung auf, die sich okklusal konisch zuspitzte. Insgesamt ergab sich hierdurch der Eindruck eines relativ homodonten Gebisses. Die Neigungswinkel der PC zur Horizontalebene des UK variierten tendenziell, was zu einer außerordentlich lückenhaften Okklusion beitrug.

Obwohl die Backenzähne nicht überdurchschnittlich eng aufeinanderfolgten, konnte bei adulten Exemplaren vielfach eine dichte Zahnstellung beobachtet werden. Diese enge Stellung war eindeutig sekundär durch übermäßige Ablagerungen im Wurzelbereich entstanden: die Wurzeln nahmen mit dem Alter an Umfang zu, bis sie zusammenstießen. Nach F. D. Kapel in Duguy und Robineau (1992) handelt es sich hierbei um Zementablagerungen. Verglichen mit den PC subadulter Individuen wirkten die PC ausgewachsener Tiere im Wurzelbereich wie aufgepumpt (Abb. 2 b). Die PC5 und gelegentlich auch die PC4 besaßen in einigen Fällen eine doppelte Wurzel. Allgemein war bei diesen beiden letzten PC das Verwachsen einer doppelten zu einer einfachen Wurzel schwächer ausgeprägt als bei den PC2–3.

Anomalien: Die beschriebenen Klappmützenschädel wiesen Abweichungen in allen Kategorien auf. Stellungsanomalien wurden jedoch aus den eingangs erwähnten Gründen nicht registriert. Überzählige Zähne (45 PC und 3 I) erschienen häufig als reduzierte PC1 in lingualen oder buccalen Lagen (Abb. 1 a). Bei einem ♂ standen 3 extrem reduzierte PC^1 (∅: 2 mm) buccal dicht an dem normal entwickelten PC^1 (ZMA 18061). Überzählige PC konnten jedoch auch als geringfügig reduzierte oder normalgroße Zahntypen sowohl lateral außerhalb als auch innerhalb der Zahnreihen auftreten. Ein UK wies eine abnorme Vergrößerung eines überzähligen I_1 auf, von der auch der ‚normale' I_1 betroffen war (ZMA 18109/19, ♂). Bei zwei weiteren UK besaßen die überzähligen Incisiven normale Abmessungen.

Insgesamt wurden 25 fehlende PC registriert. Die Anzahl der nicht angelegten Zähne eines Gebisses betrug maximal 4 PC (ZMA 18083), wobei pro Quadrant nie mehr als 1 PC fehlte. In den meisten Fällen war der Typus (PC2–5) nicht rekonstruierbar, weil die vorhandenen 4 PC lückenlos aneinander anschlossen. Selbst bei fehlendem PC_1 folgte der PC_2 unmittelbar auf den Caninus. Der UK eines ♀ wies eine Lücke zwischen dem PC_3 und dem PC_5 auf. Die Zahnreihe war in diesem Bereich glatt verwachsen, was auf einen fehlenden PC_4 schließen ließ (ZMA 18098). Bei 4 Exemplaren mit fehlenden PC war jeweils einer der übrigen PC desselben Quadranten überlang. Die Länge dieser Backenzähne entsprach etwa der zweier einzelner PC: möglicherweise sind hier während der Odontogenese zwei benachbarte Zahnkeime miteinander fusioniert. Überlange PC traten jedoch auch bei einem vollständigen und 3 polydonten Gebissen auf (ZMA 18109/164, 18109/179, 18109/311 und 18081).

Als weitere Formabweichungen wurden 2 abnorm kleine PC, 6 PC mit überdimensionalen oder fehlenden Kronen und 1 hypoplastischer PC_5 gefunden. In sechs Fällen besaß der PC_2 die Form eines PC_1. Zwei dieser PC_1-Typen waren überzählige Zähne (hier standen also drei PC_1 zwischen Caninus und PC_3). Bei zwei UK bestand der PC_5 aus 2 separaten Einzelzähnen halber PC-Länge (ZMA 18573/19 und 18573/6). Als Einzelfall unter den Formvariationen wurde ein normalgroßer PC_2 eines ♀ gefunden, der in Längsrichtung mit einem PC halber Normlänge verwachsen war (ZMA 18109/200, Abb. 2 c).

Die beiden Zähne in abnormen Positionen lateral außerhalb der Zahnreihe, ein Incisivus und ein PC, gehörten zu Gebissen ohne numerische Abweichungen (ZMA 16449 und 18109/95).

In einem einzelnen Quadranten wurden maximal 5 Zähne mit Anomalien festgestellt (ZMA 18573/49, ♀). Ein anderer UK war von 3 verschiedenen Abweichungstypen betroffen: er besaß einen überzähligen PC_1, einen überlangen PC_3 und einen fehlenden PC (ZMA 18109/179, ♀).

Abweichungen pro Individuen

Faßt man die einzelnen Abweichungskategorien als potentielle Anomalien eines individuellen Gebisses zusammen, so zeigen die ermittelten Gesamthäufigkeiten erhebliche artspezifische Unterschiede (Tab. 2). Hierbei stehen sich Seehunde (3,9%) und Bartrobben (29,4%) als Extreme eines mittleren Bereichs mit annähernd gleichen Häufigkeiten (14,4–16,7%) gegenüber. Selbstverständlich hängen diese Werte entscheidend von den Definitionen der einzelnen Kategorien ab. Klappmützen hätten zum Beispiel eine höhere Gesamtabweichungsfrequenz, wenn ihre Stellungsanomalien nicht als Trend, sondern prozentual erfaßt worden wären. Entsprechend geringer würde die Gesamthäufigkeit der Sattelrobben ausfallen, falls freiliegende Wurzeln oder vierzackige PC1 als unerhebliche morphologische Variationen außer Betracht blieben.

Abweichungen pro Quadranten

Die prozentuale Berechnung von abnormen Kieferquadranten hat in Anbetracht der zum Teil unvollständigen Sammlungen in erster Linie die Aufgabe, die Abweichungshäufigkeiten der Klappmützen-Gebisse zu relativieren (Tab. 2). Als Folge erhalten nicht Bartrobben, sondern Klappmützen die höchste Gesamthäufigkeit, was einer vergleichenden Darstellung der Befunde am ehesten gerecht wird. Unter den übrigen Arten bleiben die Relationen der Häufigkeiten im großen und ganzen gleich.

Eine Veränderung der Werte, wie etwa die vergleichsweise leicht erhöhten Gesamthäufigkeiten der Kegelrobben oder die extremen geschlechtsspezifischen Relationen bei Ringel- und Sattelrobben, wird in erster Linie durch die geringe Anzahl der Objekte verursacht: hier kann ein einzelner Schädel mit fehlenden Mandibeln bereits eine erhebliche Verschiebung der Relationen bewirken. Aus dem gleichen Grund verschwindet bei der Quadrantendarstellung das ‚Mittelfeld‘ mit einer mehr oder weniger homogenen Häufigkeitsverteilung.

Interspezifsche Schwankungen

Auch wenn man die Abweichungstypen einzeln betrachtet, fällt eine ungleiche Verteilung der Häufigkeiten auf. Für jede Art existiert ein eigenes, charakteristisches ‚Abweichungsmuster‘, durch das sie sich von den anderen Arten unterscheidet (Tab. 1, 2):

Bei *Phoca vitulina* traten keine topographischen Anomalien auf. Gebißabweichungen kamen bei ♂♂ mehr als doppelt so häufig vor wie bei ♀♀.

Ringelrobben-♂♂ waren ebenfalls wesentlich häufiger von Anomalien betroffen als ♀♀. Es konnten keine überzähligen Zähne und Stellungsanomalien registriert werden.

Fehlende Zähne scheinen bei *P. hispida* vergleichsweise häufig vorzukommen. Allerdings dürften die zum Teil extremen Werte in den Einzelkategorien (wie auch bei den Bartrobben) auf der geringen Probenanzahl beruhen.

Mit 3,4% Gesamthäufigkeit bei den ♀♀ gegenüber 11,0% bei den ♂♂ wiesen die Sattelrobben als dritte *Phoca*-Art eine ausgeprägt ungleiche geschlechtsspezifische Verteilung auf. Weibliche Tiere besaßen weder numerische noch topographische Anomalien: von den fünf Standardabweichungen war hier lediglich eine Kategorie vertreten (1 abnorm geformter PC).

Bis auf zwei Ausnahmen (1 überzähliger und 1 abnormer PC im UK) traten alle Anomalien im OK auf. Die nur bei *P. groenlandica* wahrgenommenen lateral freiliegenden Wurzeln einiger PC können sicherlich als arttypische Abweichung betrachtet werden, die auf die charakteristische Morphologie der dünnen, aufgefalteten Zahnreihen zurückzuführen ist. Da immerhin 4 von insgesamt 73 Individuen hiervon betroffen waren, wurden die art- und geschlechtsbezogenen Gesamthäufigkeiten durch diesen Abweichungstypus entscheidend erhöht.

Stewart und Stewart (1987 a), die 2 267 Mandibeln nordwestatlantischer Sattelrobben untersuchten, stellten in drei Abweichungskategorien keine signifikanten Häufigkeitsunterschiede zwischen den Geschlechtern fest. Sie fanden 1,7% überzählige Zähne, 0,5% fehlende Zähne und 0,6% Formabweichungen. Es ist wenig wahrscheinlich, daß die abweichenden Ergebnisse dieser Studie auf geographische Variationen bei Sattelrobben zurückzuführen sind. Daher muß hieraus geschlußfolgert werden, daß diesbezügliche Untersuchungen mit einem Probenumfang von N < 150 nur unter Vorbehalt interpretierbar sind.

Dieser Vorbehalt gilt auch für die untersuchten Bartrobben (N = 17). Die beschriebenen Schädel scheinen eine Neigung zu überzähligen Zähnen anzudeuten. Stewart und Stewart (1987 a) erwähnen, daß Dentitionsanomalien, insbesondere überzählige PC und fehlende Incisivi, bei *Erignathus barbatus* relativ häufig auftreten.

Auffällig für Kegelrobben war das Vorkommen von topographischen Anomalien. Oligodontie konnte in keinem Fall festgestellt werden. Die geschlechtsbezogenen Häufigkeiten waren annähernd gleichverteilt.

Bei Klappmützen fanden sich Abweichungen aller Kategorien (wenn man die tendenziell auftretenden Stellungsvariationen mitberücksichtigt), von der ♀♀ und ♂♂ gleichermaßen betroffen waren. Besonders häufig konnten überzählige Zähne (in den UK) gefunden werden. Der Trend zu abnormen Zahnstellungen schien hauptsächlich mit dem überproportionalen Wachstum der Wurzeln zusammenzuhängen. Dieses ‚sekundäre Dickenwachstum' der Wurzeln wird nicht von einem gleichstarken Wachstum der Mandibeln begleitet (siehe Keil 1966). Folglich stoßen die PC ab einem bestimmten Alter im Wurzelbereich zusammen, was wiederum die Neigung oder Verschiebung einzelner Zähne zur Folge haben kann. Daß das Volumenwachstum des Kiefers in der Lage ist, mit zunehmenden Alter eine enge Zahnstellung auszugleichen, konnte bei allen anderen untersuchten Arten, vor allem jedoch bei *P. vitulina*, beobachtet werden (siehe auch Ooë und Esaka 1981).

Diskussion

Als mögliche Ursachen für die markanten interspezifischen Schwankungen können zum Teil sicherlich die jeweils arteigenen Besonderheiten der Schädelmorphologie in Betracht gezogen werden. So unterscheidet sich die Spezies mit den meisten Abweichungstypen und der höchsten Gesamthäufigkeit, *C. cristata*, im proportionalen Aufbau des Schädels auffällig von den anderen fünf Arten: den langgestreckten, kräftigen Mandibeln und seinen rostrad verschobenen Zahnreihen steht ein Oberschädel mit bemerkenswert kurzem Oberkiefer gegenüber – die Schnauze ist unterproportional verkürzt. Die besondere Form

der Mandibeln erklärt sich aus dem charakteristischen Aufbau der Schädelbasis, wo dem verkürzten Rostrum breite, ausladend geschwungene Jochbögen und ein kräftg entwickeltes Hinterhauptsgelenk folgen. Um in die Gelenkgrube zu passen, müssen die Mandibeln entsprechend langgestreckt sein, während eine opponente Zahnstellung eine Verschiebung des Gebisses in den rostralen Bereich erforderlich macht. Es liegt auf der Hand, daß eine neotene Verkürzung des Schädels, wie sie bei *C. cristata* möglicherweise vorliegt, eine tiefgreifende Veränderung der Gebißanlage impliziert.

Ein weiterer Faktor, der den Aufbau eines Gebisses mitgestaltet, ergibt sich aus dem jeweiligen Selektionsdruck auf die Funktionalität der Zähne. Um schnelle, wendige Beute fangen zu können, ist das Greif- und Fixiervermögen des Gebisses von entscheidender Wichtigkeit (Loughlin 1982). Spitze und gezackte Zähne sind daher typisch für Fischfresser. Das tendenziell homodonte Gebiß der Klappmützen mit seinen verhältnismäßig stumpfen PC eignet sich besonders zum Zerkleinem von Crustaceen und Mollusken. Von *E. barbatus* ist bekannt, daß adulte Tiere trotz völlig abgenutzter oder komplett ausgefallener Zähne in der Lage sind, sich mit einer ihrem Lebensunterhalt genügenden Nahrungsmenge zu versorgen (Mohr 1952; Ridgway und Harrison 1981). Der selektive Druck auf ein funktionelles Gebiß ist in diesem Fall offensichtlich gering. Lönnberg (1922) stellte fest, daß *Phoca hispida botnica* allgemein robustere und dickere Zähne besitzt als seine arktischen Verwandten (*P. h. hispida*). Er nahm an, daß die Entwicklung eines qualitativ besseren Gebisses bei bottnischen Ringelrobben durch einen stärkeren selektiven Stimulus erfolgt.

Weder morphologische noch ethologische Besonderheiten scheinen allerdings das vergleichsweise außerordentlich geringe Vorkommen von Anomalien bei *P. vitulina* erklären zu können. Möglicherweise ist die Abweichungsfrequenz in diesem Fall mit dem Verbreitungsgebiet der Seehunde korreliert:

P. vitulina hat von den sechs untersuchten Arten das südlichste Verbreitungsgebiet. Die durchschnittlich höhere Umgebungstemperatur könnte sich im Hinblick auf Gebißabweichungen günstiger auf die Ontogenese der Seehunde auswirken. Newell (1949) nimmt an, daß niedrige Temperaturen eine Retardation der somatischen Entwicklung begünstigen. Das fötale Wachstum scheint bei arktischen Robben entscheidend von der Speckschicht des schwangeren ♀ abzuhängen (Stewart und Stewart 1989). Diese Isolierschicht muß bei einer Körpertemperatur von 37 °C und Außentemperaturen um –30 °C einem Temperaturgefälle von fast 70 °C standhalten können. Der Aufbau und die Dicke dieser Schicht ist wiederum abhängig von diversen Umgebungsfaktoren (Nahrungsangebot, Eisdicke, Wetterverhältnisse, etc.).

Für adulte Robben sind periodische, saisonale Schwankungen des Zahnwachstums bekannt, wobei die Stärke der Dentinablagerungen direkt vom Nahrungsangebot abzuhängen scheint (Keil 1966). Bei morphologischen Messungen an Sattelrobbenjungen in den Jahren 1982 und 1984 stellten Stewart und Stewart (1987 b) fest, daß die Zähne schon bei Juvenilen unterschiedlich groß entwickelt sein können. Es ist vorstellbar, daß ökologische Faktoren nicht nur das Zahnwachstum beeinflussen, sondern bereits während der Odontogenese eine prägende Rolle spielen.

Es gibt bei Robben jedoch nicht nur Hinweise für retardierte, sondern auch für akzelerierte Ontogeneseabläufe: der frühe Gebißwechsel, der gewöhnlich intrauterin erfolgt, ist ebenso ein Anzeichen für einen beschleunigten Entwicklungsablauf wie die Verkürzung der Laktationsphase (Wyss 1994; Slaughter et al. 1974).

Wahrscheinlich unterscheiden sich derartige heterochrone Mechanismen interspezifisch in kleinen, aber wichtigen Details. Das kann zum einen bedeuten, daß Art A stärker von einer heterochronen Entwicklung betroffen ist als Art B. Zum anderen können artspezifisch jeweils unterschiedliche Bereiche einer Entwicklungsverschiebung unterliegen, so daß etwa ein relativ schnelleres Wachstum der Maxillaria gegenüber den Mandibeln stattfindet. In einem solchen Fall wäre eine unterschiedliche Abweichungsverteilung in

den Kieferhälften zu erwarten, wie es bei *P. groenlandica* der Fall ist (SUZUKI et al. 1990; WOLSAN 1984).

Das Verbreitungsgebiet der Kegelrobben stimmt (bis auf die westatlantischen Areale) annähernd mit dem der Seehunde überein. Da sowohl die Gesamthäufigkeiten als auch die betroffenen Einzelkategorien beider Arten stark voneinander abweichen, wird deutlich, daß die Umgebungstemperatur keine absolute, sondern eine mögliche Komponente im Zusammenspiel verschiedener Einflußfaktoren darstellt.

Als weitere auslösende Faktoren bei der Spaltung eines Zahnkeims – und damit bei der Entwicklung eines überzähligen Zahns – werden zum Beispiel Infektionen oder Mangelerscheinungen (Vitamin A) vermutet (WOLSAN 1984). Über den Einfluß physiologischer Faktoren (Zeitpunkt und/oder Dauer von Östrus, Tragzeit, Laktation etc.) auf die Zahnentwicklung ist bislang noch wenig bekannt. Auch dürfte in diesem Zusammenhang interessant sein, inwieweit die verschiedenen Toxikanten, die in Geweben und Organen von Robben nachgewiesen worden sind, den Ablauf der Odontogenese beeinflussen (DUGUY und ROBINEAU 1992).

Es existiert eine beträchtliche Anzahl von Hypothesen und Entstehungsmodellen, die sich dem Auftreten überzähliger Zähne bei Robben widmen (SAHLERTZ 1898; LÖNNBERG 1922; MOHR 1952; STEWART und STEWART 1987b; SUZUKI et al. 1990). Oft wird suggeriert, daß die Morphologie der Robben als eine evolutionäre Momentaufnahme aufzufassen ist, deren weiterentwickelte Form den Walen ähneln könnte. Man stellt sich in diesem Fall eine allmähliche Verlängerung des Rostrums vor, die von einer zunehmenden Poly- und Homodontie des Gebisses begleitet wird (MOHR 1982).

FUJITA, zitiert in SUZUKI et al. (1990), vermutet, daß überzählige Zähne bevorzugt in den freien Zwischenräumen aufeinanderfolgender Zahnkeime entstehen: der zusätzliche Keim benötigt für seine Morphogenese einen genügend großen Freiraum. Ein akzeleriertes Längenwachstum der Kiefer und der Zahnreihen, das solche Zwischenräume entstehen läßt, könnte demzufolge mit dem symmetrischen Auftreten überzähliger Zähne korreliert sein (siehe auch LÖNNBERG 1922).

In der Literatur wird oft erwähnt, daß überzählige Zähne bei Robben häufiger auftreten als fehlende (COLYER 1936; KEIL 1966). Falls die phylogenetische Entwicklung der Pinnipedia tatsächlich parallel mit der Phylogenese der Wale verläuft, wäre in der Tat ein relativ höherer Anteil überzähliger Zähne gegenüber den übrigen Abweichungstypen zu erwarten.

Die Ergebnisse dieser Untersuchung liefern – für die derzeitige Entwicklungsphase der Pinnipedia – diesbezüglich keinerlei stichhaltige Hinweise (wenn man *E. barbatus* außer Betracht läßt). Bei *P. vitulina* und *P. hispida* überwiegt der Anteil abwesender Zähne, was theoretisch auf eine Reduktion des Gebisses hindeutet.

Lediglich das Abweichungsprofil von *P. groenlandica* würde mit der Hypothese übereinstimmen: es konnten keine fehlenden Zähne gefunden werden und bis auf eine Ausnahme waren alle überzähligen Zähne als terminale PC6 in den Verlauf der Zahnreihen integriert.

Zwar gilt dieser Sachverhalt auch für *H. grypus*, doch stellen die 2 überzähligen PC einer einzelnen Kegelrobbe von insgesamt 54 untersuchten Schädeln eine etwas dürftige Grundlage für Spekulationen dar. Eine weitere Art mit einem hohen Anteil überzähliger Zähne, *C. cristata*, besitzt merkwürdigerweise ein ausgesprochen kurzes Rostrum. Diese Verkürzung scheint auf eine neotene Retardation hinzudeuten, wodurch das Cranium ein juveniles Erscheinungsbild erhält (WYSS 1994).

Alles in allem scheinen somit bei der Schädelentwicklung der Robben zwei entgegengerichtete Prozesse wirksam zu sein: Akzeleration und Retardation (siehe auch WYSS 1994). Auch wenn beide Mechanismen während der Ontogenese theoretisch gleichzeitig auftreten können, bleibt aus evolutionärer Sicht ein interessanter Aspekt bestehen: der akzelerierten Verlängerung des Rostrums steht als evolutionärer Trend eine retardierte rostrale Verkürzung gegenüber.

Zusammenfassung

Bei sechs nordatlantischen Robbenarten wurden Oberschädel und Mandibeln auf Gebißanomalien untersucht. Unter den 1 006 Exemplaren befanden sich 526 Klappmützen (*Cystophora cristata*), 305 Seehunde (*Phoca vitulina*), 73 Sattelrobben (*Phoca groenlandica*), 54 Kegelrobben (*Halichoerus grypus*), 31 Ringelrobben (*Phoca hispida*) und 17 Bartrobben (*Erignathus barbatus*). Die Abweichungen wurden, nach Geschlechtern getrennt, in die folgenden sechs Kategorien eingeteilt: überzählige Zähne, fehlende Zähne, Formvariationen der Zähne, Stellungsanomalien, Positionsanomalien und sonstige, außergewöhnliche Anomalien. Da die Sammlung der Klappmützenexemplare überwiegend aus einzelnen Mandibeln bestand, wurden neben den Abweichungshäufigkeiten pro Individuen auch die Anteile der Anomalien pro Quadranten berechnet. Die Gesamthäufigkeiten (Abweichungen aller Kategorien zusammengenommen) pro Quadranten betrugen:

1,6% (*P. vitulina*), 5,6% (*P. hispida*), 6,6% (*P. groenlandica*), 8,3% (*H. grypus*), 11,8% (*E. barbatus*) und 13,2% (*C. cristata*). Diese bemerkenswerten interspezifischen Schwankungen wurden von unterschiedlichen prozentualen Anteilen in den einzelnen Kategorien begleitet. Hierdurch konnte hinsichtlich Topographie, Typus und Anzahl der betroffenen Zähne für jede Spezies ein charakteristisches, arteigenes Abweichungsmuster festgestellt werden.

Danksagung

Wir danken Dr. C. Smeenk für seine Unterstützung bei der Untersuchung der Pinnipedia-Sammlung des ‚Nationaal Natuurhistorisch Museum‘ in Leiden. Besonderer Dank gebührt E. J. O. Kompanje, der seine freie Zeit opferte, um die Auswertung der Sammlung des Rotterdammer ‚Natuur Museum‘ zu ermöglichen.

Literatur

Bateson, W. (1892): On numerical variation in teeth, with a discussion of the conception of homology. Proc. Zool. Soc. Lond. **1892**, 102–115.

Bree, P. J. H. van; Sinkeldam, E. J. (1969): Anomalies in the dentition of the fox, *Vulpes vulpes* (Linnaeus, 1758), from continental western Europe. Bijdr. Dierk. (Amsterdam) **39**, 3–5.

Burns, J. J.; Fay, F. H. (1970): Comparative morphology of the skull of the Ribbon seal, *Histriophoca fasciata*, with remarks on sytematics of Phocidae. J. Zool. (London) **161**, 363–394.

Colyer, F. (1936): Variations and diseases of the teeth of animals. London: John Bale, Sons and Danielsson, Ltd.

Duguy, R.; Robineau, D. (Hrsg.) (1992): Handbuch der Säugetiere Europas. Band 6: Meeressäuger. Teil II: Robben-Pinnipedia. Wiesbaden: Aula-Verlag.

Jentink, F. A. (1887): Catalogue Ostéologique. Leiden: E. J. Brill.

Keil, A. (1966): Grundzüge der Odontologie. Allgemeine und vergleichende Zahnkunde als Organwissenschaft. Berlin-Nikolassee: Gebr. Borntraeger.

King, J. E. (1991): Seals of the world. 2nd ed. New York, Ithaka: Cornell Univ. Press.

Lönnberg, E. (1922): On some anomalies in the dentition of *Phoca hispida*. Bijdr. Dierk. (Amsterdam) **22**, 169–173.

Loughlin, T. R. (1982): Functional adaptation of eruption sequence of pinniped postcanine teeth. J. Mammalogy **63**, 523–525.

Lüps, P. (1990): Untersuchungen am P1 im Gebiß des europäischen Dachses (*Meles meles*). Z. Säugetierkunde **55**, 16–27.

Mohr, E. (1952): Die Robben der europäischen Gewässer. Frankfurt/Main: Verlag Dr. Paul Schöps.

Neuenschwander, A.; Lüps, P. (1975): Zahnvariationen bei einer Mauswiesel-Population, *Mustela nivalis* Linné, 1766, aus Hessen. Säugetierkundl. Mitt. **23**, 85–93.

Newell, N. D. (1949): Phyletic size increase, an important trend illustrated by fossil invertebrates. Evolution **3**, 103–124.

Ooë, T.; Esaka, S. (1981): Le chevauchement des dents jugales chez les phoques: modalités et évolution postnatale. Mammalia **45**, 497–503.

Ridgeway, S. H.; Harrison, R. J. (eds) (1981): Handbook of marine mammals. Vol. 2 Seals. London, New York, Toronto, Sydney, San Francisco: Academic Press.

Sahlertz, I. (1898): Notiz über retardirte Milchzähne. Zool. Anz. **1**, 338–340.

Slaughter, B. H.; Pine, R. H.; Pine, N. E. (1974): Eruption of cheek teeth in Insectivora and Carnivora. J. Mammalogy **55**, 115–125.

Suzuki, M.; Ohtaishi, N.; Nakane, F. (1990): Supernumerary postcanine teeth in the Kuril seal (*Phoca vitulina*), the larga seal (*Phoca largha*) and the ribbon seal (*Phoca fasciata*). Jpn. J. Oral Biol. **32**, 323–329.

Stewart, R. E. A.; Stewart, B. E. (1987 a): Mandibular dental anomalies of Northwest Atlantic harp seals, *Phoca groenlandica.* Can. J. Zool. **65**, 769–771.

Stewart, R. E. A.; Stewart, B. E. (1987 b): Dental ontogeny of harp seals, *Phoca groenlandica.* Can. J. Zool. **65**, 1425–1434.

Stewart, R. E. A.; Stewart, B. E. (1989): Fetal growth of Northwest Atlantic harp seals, *Phoca groenlandica.* Can. J. Zool. **67**, 2147–2157.

Wolsan, M. (1984): The origin of extra teeth in mammals. Acta theriol. **29**, 128–133.

Wyss, A. R. (1994): The evolution of body size in phocids: some ontogenetic and phylogenetic observations. Proc. San Diego Soc. Nat. Hist. **29**, 69–75.

Anschr. der Verf.: Stefan Könemann und Dr. Peter J. H. van Bree, Zoölogisch Museum, Universiteit van Amsterdam, Mauritskade 61, NL-1092 AD Amsterdam, Nederland.

Z. Säugetierkunde **62** (1997) 86–92

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Bat predation by small carnivores in a central African rainforest

By R. Hutterer and Justina C. Ray

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn and Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, USA

Receipt of Ms. 04. 04. 1996
Acceptance of Ms. 22. 06. 1996

Abstract

Fragments of four species of bats (*Mops* cf. *spurrelli*, *Nycteris arge*, *Hipposideros cyclops*, *H. ruber*) were identified in scats of small carnivores collected in a tropical rainforest of Central African Republic. For all four species the Dzanga forest constitutes the second locality record in this country. Genets (*Genetta servalina*) and long-nosed mongoose (*Herpestes naso*) were identified as the predator species. Bats occurred in only 0.4% of the scats analyzed. The few examples refer to bat species which roost solitarily or in small groups. Their presence in the scats can be attributed to chance encounters. Large bat colonies seem to be rare or inaccessible in the study area.

Introduction

Bats are rarely common food items in the diets of mammals, with the exception of other bats such as false vampires (*Megaderma* in Asia, *Macroderma* in Australia, *Vampyrum* in South America) which are known to prey upon the smaller members of their order (Hill and Smith 1984). Other mammals, such as opossums, lorises, and a number of carnivores, probably take live bats only when captured in chance encounters or when found on the floor of caves and other roosts (Hill and Smith 1984). Although mammalian carnivores are assumed to be predators of bats (Rosevear 1965; Gilette and Kimbrough 1970; Bekker and Mostert 1991), there has been little evidence of this in the literature, apart from anecdotal observations. Very little is known about predation of bats by carnivores in tropical Africa. In this study we document four cases where bat remains were found in the scats of genets and mongooses in a central African rainforest. In addition, we discuss the ecological conditions that may lead to encounters between bats and small carnivores.

Material and methods

Small carnivores were studied by JCR from 1992–1994 in the Dzanga-Sangha Reserve of south-western Central African Republic. The species studied include *Genetta servalina*, *Herpestes naso*, *Atilax paludinosus*, *Bdeogale nigripes*, *Nandinia binotata*, *Civettictis civetta*, and *Profelis aurata*. The 35 km^2 study area (Dzanga) is located in the extreme south-western corner of the Central African Republic, between the borders of Cameroon and Congo (Ray 1995, 1996). The base camp, in the Dzanga-Sangha Special Dense Forest Reserve and Dzanga-Ndoki National Park, was 35 km from the village of Bayanga. Human population in the area is low with less than one person/km^2.

The study area was a mosaic of five principal habitat types: mixed-species semi-deciduous unlogged forest, selectively logged forest, second-growth forest along secondary logging roads, mono-dominant

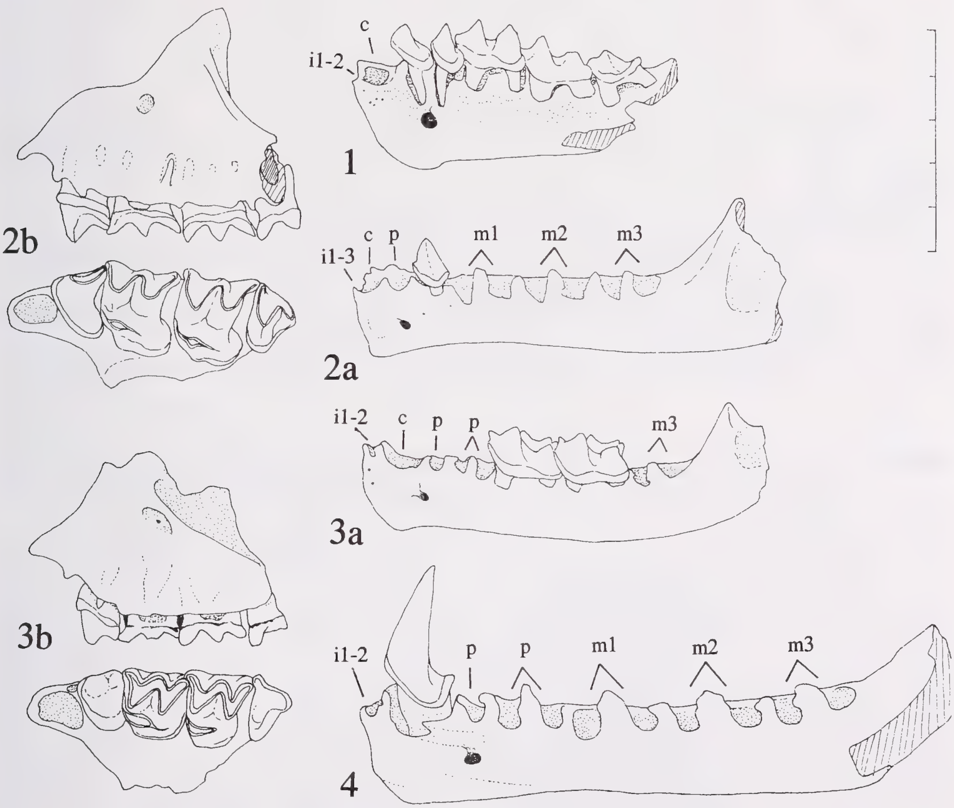
Gilbertiodendron dewevrei forest, and a thin ribbon of swamp forest bordering the Kongana stream that bisected the study area. For further details see Ray and Hutterer (1996).

Approximately 45 km of logging roads, trails, and streambeds were walked regularly by one to four individuals during a 25-month period, whereby carnivore scats were collected opportunistically. Scat identifications were made based on diameter, field signs, hair ingested while grooming, and thin layer chromatography of bile acids (Ray 1996).

Scats were washed in a fine-meshed sieve, dried in the sun or over a fire, and stored in plastic bags. Jaws and jaw fragments were identified by RH. Identification was aided by extensive comparisons with properly identified specimens in the collections of the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn (ZFMK). The nomenclature of bats follows Koopman (1993).

Results

Out of a total of 904 carnivore scats analyzed, only four contained fragments of bats (0.4%). Each yielded remains of only one individual, representing three different families and genera and four species of bats. We identified them as *Mops* cf. *spurelli* (Dollman, 1911) (scat no. 75: fragment of left mandible), *Nycteris arge* Thomas, 1903 (scat no. 436: fragments of left mandible and maxillary), *Hipposideros ruber* (Noack, 1893) (scat



Figs. 1–4. Skull fragments of bats found in small carnivore scats collected in the Dzanga area, C.A.R. 1: *Mops* cf. *spurelli* (left lower mandible), 2 a, b: *Nycteris arge* (left lower mandible, left maxillary with P4-M3), 3 a, b: *Hipposideros ruber* (left lower mandible, left maxillary with P4-M3), 4: *Hipposideros cyclops* (right lower mandible, reversed). Corresponding teeth are noted for the alveoli of the mandible. Scale is 5 mm.

no. 438: left and right mandibles, 2 maxillary fragments), and *Hipposideros cyclops* (Temminck, 1853) (scat no. 843: left and right mandibles, 1 upper canine).

Mops cf. *spurrelli* (Molossidae) was identified by the short and stout mandible and by the broad and heavy dentition (Fig. 1), and by comparison with figures and measurements provided by Freeman (1981). It must be noted, however, that *Mops nanulus* is very similar, if not conspecific (Koopman 1989), and that a discrimination between the two forms on the basis of a mandibular fragment may not be possible. The latter species, however, has not yet been recorded from C.A.R. The bat was probably taken by a genet (*Genetta servalina*); the scat also contained traces of arthropods and remains of blue duiker (*Cephalophus monticola*) and porcupine (*Atherurus africanus*). In Central African Republic this molossid bat was first collected by Schlitter et al. (1982) north of M'Baiki. Our specimen is the second locality record for the country.

Nycteris arge (Nycteridae) was identified on the basis of both upper and lower skull fragments (Fig. 2). The anterior-lateral ridge of the skull (Fig. 2 b) is typical of a nycterid bat. The large size of the lower premolar (Fig. 2 a) groups it into the *Nycteris arge* group as defined by Van Cakenberghe and De Vree (1985). The group also includes *N. intermedia*, *N. nana*, and *N. major.* From these *N. arge* differs in size, the first two species being considerably smaller and the latter being larger. The Dzanga fragment fits well with specimens of *N. arge* from Cameroon and with the measurements provided by Van Cakenberghe and De Vree (1985) (Tab. 1). The carnivore species which took *Nycteris arge* could not be determined. The scat also contained arthropod remains. *N. arge* was first recorded from Salo, C.A.R., by Schlitter et al. (1982). The Dzanga specimen represents the second locality record for the Central African Republic.

The identity of *Hipposideros ruber* (Hipposideridae) was settled on the basis of tooth formula, shape of the maxillary fragment and molars (Fig. 3 b), and size and shape of the mandible (Fig. 3 a, Tab.1). Skull fragments of this species are easily mistaken for *H. beatus* or *Rhinolophus landeri*, among others. The similar-sized *Hipposideros caffer* has much smaller molars and is readily separated. A comparison of toothrow measurements (Tab. 1) shows that the fragments very likely represent *H. ruber.* However, the relations of this and other small species such as *H. lamottei* and *H. guineensis* have still to be investigated (Koopman et al. 1995). The bat was taken by a long-nosed mongoose (*Herpestes naso*); the scat also contained remains of 5 shrews (*Crocidura ludia*, 2 *C. nigrofusca*, *Suncus re-*

Table 1. Comparison of the alveolus length (mm) of upper and lower toothrow of the Dzanga bat fragments with measurements taken from museum specimens and from the literature.

	C-M3	c-m3
Mops spurrelli		
Freeman (1981) (n = 1)	5.50	6.50
Dzanga, C.A.R. (n = 1)	–	6.77
Nycteris arge		
Van Cakenberghe and De Vree (1985) (n = 134)	6.39	7.18
Dzanga, C.A.R. (n = 1)	6.54	7.07
Hipposideros ruber		
Cameroon (ZFMK, n = 7)	6.02	7.08
Dzanga, C.A.R. (n = 1)	5.93	7.12
Hipposideros cyclops		
Cameroon (ZFMK, n = 3)	9.41	10.33
Dzanga, C.A.R. (n = 1)	–	10.39

myi, *Sylvisorex ollula*; see Ray and Hutterer 1996) and some arthropods. Schlitter et al. (1982) published the first record of this species from Central African Republic (near N'dele). The Dzanga fragment therefore constitutes the second locality record for the country.

Hipposideros cyclops is documented only by mandible fragments (Fig. 4) and by an isolated upper canine. These remains indicate a very large bat, which at first sight was mistaken for *Rhinolophus maclaudi*, but the tooth formula points to genus *Hipposideros*. The specimen was probably taken by a genet; the scat in which it was found also contained a shrew (*Suncus remyi*). Only recently Hill (1983) recorded a specimen of this large bat from Bamingui-Bangoran National Park, C.A.R.; the Dzanga record therefore is the second for the country.

Discussion

Raptors are generally the most significant predators of bats (Ruprecht 1979; Tuttle and Stevenson 1982; Fenton et al. 1994), and many bats engage in energetically expensive behaviors apparently in order to avoid this threat (Krzanowski 1973; see also Tuttle and Stevenson 1982). The few accounts of predation on bats by mammalian carnivores are incidences when a regular and predictable source was available in the form of a large roost. In southern Africa, Carpenter (1970) observed a genet waiting by an opening of a house roof for the emergence of bats (*Eptesicus* and *Scotophilus* spp.) and over a five-night period the individual averaged six bats per night. On another occasion, the same author discovered a genet preying upon *Rhinolophus simulator* that were nesting in a shallow cave. Urbancyk (1981) reported a case of predation on bats by stone marten (*Martes foina*) in a wintering cave in Poland. Remains of more than 100 *Barbastella barbastellus* and 10 *Myotis myotis* (both known to roost in large assemblages) were found inside the cave, while marten faeces containing bat remains were located in the vicinity.

The predictable emergence of large colonies of bats from their roosts can provide a regular food source to opportunistic predators whose home ranges occupy the same area (Fenton et al. 1994). Given the low proportion of bats in the diet of Dzanga carnivores and the generalized nature of the food habits of most (Ray 1996), this may indicate that such large colonies were unavailable within the home ranges of animals represented by the scats collected in this study, perhaps because suitable roost sites were either absent or inaccessible. Indeed, the four bats found in carnivore scats were representatives of genera that do not tend to occur in large colonies.

Hipposideros cyclops is a large bat (mean body mass 32.2 g, n = 3, Cameroon) that roosts singly or in small groups within the cavities of hollow standing trees (Eisentraut 1942; Verschuren 1957; Brosset 1966, 1969). Members of this species are found in cavities high above the ground, which they sometimes share with flying squirrels (Anomaluridae). Roosting sites can be used continuously for many years (Brosset 1966). Although little is known about the smaller *H. ruber* (mean body mass 10.1 g, n = 10, Cameroon) and other species in the genus, it is reasonable to suggest that they have similar roost ecologies. According to Kunz (1982), small groups of *Nycteris arge*, *N. grandis*, *N. major*, and *N. nana* typically roost in trees with entrances located near the base. Verschuren (1957) found *Nycteris intermedia* and other species within cavities in trees in the Garamba National Park (Zaire). During the day, they also rest in twigs close to the ground, in ravines, and in other hidden places (Fig. 5).

Experiments have shown that roosting in large colonies decreases the risk of predator attack to any one individual (Fenton et al. 1994). This is no longer the case for bats in smaller colonies, which must utilize different behaviours such as roost switching and unpredictable and burst emergences (Morrison 1980; Fenton et al. 1985; Speakman et al.

Fig. 5. Roost sites of *Hipposideros cylops* (left) and *Nycteris* sp. (right) in the Garamba National Park, Zaire; modified after VERSCHUREN (1957).

1992; FENTON et al. 1994). Therefore, predators are less able to predictably encounter small colonies and encounter rates will probably depend on the degree of overlap of the microhabitats where the carnivores forage and the bats roost.

A genet, *Genetta servalina*, and a mongoose, *Herpestes naso*, were positively identified as predators of bats in this study. The former is a largely arboreal and nocturnal species (RAHM 1972; ROSEVEAR 1974), although it is known to sleep and hunt on or near the ground (ROSEVEAR 1974; WEMMER 1977). During the day, genets find shelter in hollow trees or logs, holes in tree trunks or in the ground, or even in dense vegetation (SMITHERS 1971; ROSEVEAR 1974). The long-nosed mongoose is strictly terrestrial and is active only during the day (RAY 1996). In the Dzanga forest the principal prey of both carnivores were arthropods, rodents, and shrews; however, the genet was somewhat less insectivorous (RAY 1996; RAY and HUTTERER 1996).

Genets may encounter bats in hollow logs or standing trees, a microhabitat that both animals utilize as daytime rest-sites. The diurnal and terrestrial long-nosed mongoose may encounter bats resting in fallen logs or in holes on the ground. Judging from scats, the favored foraging microhabitat of this forest mongoose is in areas characterized by dense understory, among leaf litter and fallen timber. As such, it may also encounter bats like *Nycteris* spp. in dense thickets that are resting on twigs close to the ground (Fig. 5). A further possibility is that these carnivores scavenged bat carcasses.

In conclusion, predation on bats by mammalian carnivores was a rare phenomenon in this central African rainforest. The few examples that we recorded can be attributed to chance encounters and are probably indicative of the paucity or inaccessibility of large bat colonies in the study area.

Acknowledgements

Field work of JCR was supported by a FULBRIGHT scholarship and grants from the Wildlife Conservation Society and the Conservation, Food and Health Foundation. MAKA SYLVESTRE, BOKOMBI FRANCO, MOKONZO ETIENNE, MOKOKO MARC, ETUBU GASTON, SINGALE JEROME, and BALAYONA JOSEPH assisted in the field. The support of Le Ministere des Eaux et Fôrets, Chasse, Peche et Tourisme and the World

Wildlife Fund R.C.A./U.S. in the Central African Republic was also invaluable. Many thanks also for the generous support of University of Florida's Center for African Studies and the Program for Tropical Conservation and Development. JAY MALCOLM, GUSTAV PETERS and HENNING VIERHAUS read drafts of the manuscript; we are grateful for their critical comments and valuable suggestions.

Zusammenfassung

Fledermäuse als Nahrung kleiner Raubtiere in einem zentralafrikanischen Regenwald

In Kotproben von Kleinraubtieren, die in einem tropischen Regenwald der Zentralafrikanischen Republik gesammelt worden waren, wurden Fragmente von vier Fledermausarten (*Mops* cf. *spurrelli*, *Nycteris arge*, *Hipposideros cyclops*, *H. ruber*) nachgewiesen. Der Dzanga-Regenwald ist für alle vier Fledermausarten der zweite Fundort in der Zentralafrikanischen Republik. Schleichkatzen (*Genetta servalina*) und Langnasenmanguste (*Herpestes naso*) wurde als zugehörige Prädatoren bestimmt. Fledermausreste fanden sich in nur 0.4% der untersuchten Proben. Die wenigen Fälle betreffen sämtlich Arten, die keine großen Kolonien bilden; ihre Erbeutung wird auf Zufallsbegegnungen zwischen Fledermäusen und Carnivoren zurückgeführt. Große Fledermauskolonien fehlen offenbar im Untersuchungsgebiet oder sind für Prädatoren unerreichbar.

References

BEKKER, J. P.; MOSTERT, K. (1991): Predatie op vleermuizen in Nederland. Lutra **34**, 1–26.

BROSSET, A. (1966): Les chiroptères du Haut-Ivindo (Gabon). Biol. Gabon. **2**, 47–86.

BROSSET, A. (1969): Recherches sur la biologie des chiroptères troglophiles dans le nord-est du Gabon. Biol. Gabon. **2**, 93–116.

CARPENTER, G. P. (1970): Some observations on the Rusty-spotted Genet (*Genetta rubiginosa zuluensis*). Lammergeyer **11**, 60–63.

EISENTRAUT, M. (1942): Beitrag zur Oekologie Kameruner Chiropteren. Mitt. Zool. Mus. Berlin **25**, 245–275.

FENTON, M. B.; BRIGHAM, R. M.; MILLS, A. M.; RAUTENBACH, I. L. (1985): The roosting and foraging areas of *Epomophorus wahlbergi* (Pteropodidae) and *Scotophilus viridis* (Vespertilionidae) in Kruger National Park, South Africa. J. Mammalogy **66**, 461–468.

FENTON, M. M.; RAUTENBACH, I. L.; SMITH, S. E.; SWANEPOEL, C. M.; GROSELL, J.; VAN JAARSVELD, J. (1994): Raptors and bats: threats and opportunities. Anim. Behav. **48**, 9–18.

FREEMAN, P. W. (1981): A multivariate study of the family Molossidae (Mammalia, Chiroptera): morphology, ecology, evolution. Fieldiana Zool. N.S. **7**, 1–173.

GILETTE, D. D.; KIMBROUGH, J. D. (1970): Chiropteran mortality. In: About bats. Ed. by B. H. SLAUGHTER and D. W. WALTON. Dallas: Southern Methodists Univ. Pp. 262–283.

HILL, J. E. (1983): Further records of bats from Central African Republic (Mammalia: Chiroptera). Ann. Carnegie Mus. **52**, 55–58.

HILL, J. E.; SMITH, J. D. (1984): Bats, a natural history. London: British Museum (Natural History).

KOOPMAN, K. F. (1989): Systematic notes on Liberian bats. Amer. Mus. Novit. **2946**, 1–11.

KOOPMAN, K. F. (1993): Order Chiroptera. Mammal species of the world, a taxonomic and geographic reference. Ed. by D. E. WILSON and D. A. REEDER. Washington: Smithsonian Institution Press. Pp. 137–241.

KOOPMAN, K. F.; KOFRON, C. P.; CHAPMAN, A. (1995): The bats of Liberia: systematic, ecology, and distribution. Amer. Mus. Novit. **3148**, 1–24.

KRZANOWSKI, A. (1973): Numerical comparison of Vespertilionidae and Rhinolophidae (Chiroptera: Mammalia) in the owl pellets. Acta zool. cracov. **18**, 133–140.

KUNZ, T. H. (1982): Roosting ecology of bats. In: Ecology of bats. Ed. by T. H. KUNZ. New York: Plenum. Pp. 1–55.

MORRISON, D. W. (1980): Foraging and day roosting dynamics of canopy fruit bats in Panama. J. Mammalogy **61**, 20–29.

RAHM, U. (1972): Zur Verbreitung und Ökologie der Säugetiere des afrikanischen Regenwaldes. Acta Tropica **29**, 459–472.

Ray, J. C. (1995): The life in sympatry of *Xenogale naso* and *Atilax paludinosus* in a central African forest. Small Carnivore Conservation **12**, 1–4.

Ray, J. C. (1996): Resource use patterns among mongooses and other carnivores in a central African rainforest. Ph.D. Diss., Univ. of Florida, Gainesville, FL.

Ray, J. C.; Hutterer, R. (1996): Structure of a shrew community in Central African Republic based on the analysis of carnivore scats, with the description of a new *Sylvisorex* (Mammalia: Soricidae). Ecotropica **1**, 85–97.

Rosevear, D. R. (1965): The bats of West Africa. London: British Museum (Natural History).

Rosevear, D. R. (1974): The carnivores of West Africa. London: British Museum (Natural History).

Ruprecht, A. L. (1979): Bats (Chiroptera) as constituents of the food of barn owls *Tyto alba* in Poland. Ibis **121**, 489–494.

Schlitter, D. A.; Robbins, L. W.; Buchanan, S. A. (1982): Bats of the Central African Republic (Mammmalia: Chiroptera). Ann. Carnegie Mus. **51**, 133–155.

Smithers, R. H. N. (1971): The mammals of Botswana. Natl. Mus. Rhodesia, Mus. Memoir **4**, 1–340.

Speakman, J. R.; Bullock, D. J.; Eales, L. A.; Racey, P. A. (1992): A problem defining temporal pattern in animal behaviour: clustering in the emergence behaviour of bats from maternity roosts. Anim. Behav. **43**, 491–500.

Tuttle, M. D.; Stevenson, D. (1981): Growth and survival of bats. In: Ecology of bats. Ed. by T. H. Kunz. New York: Plenum. Pp. 105–150.

Urbanczyk, Z. (1981): Fledermäuse (Chiroptera) in der Nahrung des Marders (*Martes* spec.). Säugetierkdl. Mitt. **29**, 77–79.

Van Cakenberghe, V.; De Vree, F. (1985): Systematics of African *Nycteris* (Mammalia: Chiroptera). In: Proceedings of the International Symposium on African vertebrates: sycstematics, phylogeny and evolutionary ecology. Ed. by K.-L. Schuchmann. Bonn: Zoologisches Forschungsinstitut und Museum A. Koenig. Pp. 53–90.

Verschuren, J. (1957): Ecologie, biologie et systématique des Cheiroptères. Exploration du Parc National de la Garamba **7**, 1–474.

Wemmer, C. M. (1977): Comparative ethology of the large-spotted genet (*Genetta tigrina*) and some related viverrids. Smiths. Contr. Zool. **239**, 1–93.

Authors' addresses: Dr. Rainer Hutterer, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany; Dr. Justina C. Ray, Faculty of Forestry, University of Toronto, Toronto, Ontario, Canada M5S 3B3.

Z. Säugetierkunde **62** (1997) 93–98

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

A causal analysis of the relationships between behaviour patterns of free living warthogs

M. J. Somers and O. Anne E. Rasa

Centre tor Wildlife Management, University of Pretoria, Pretoria, South Africa and Abteilung Ethologie, Zoologisches Institut, Universität Bonn, Bonn, Germany

Receipt of Ms. 06. 04. 1995
Acceptance of Ms. 20. 09. 1996

Abstract

Studied were, using factor and concordance analysis, the causal relationships between behaviour patterns of free living warthogs *Phacochoerus aethiopicus* in the Andries Vosloo Kudu Reserve, Eastern Cape Province, South Africa. Warthog behaviour patterns fall into five categories with similar causal relationships, the first two broad categories consisting of social behaviours, a third large category comprising comfort behaviour patterns, the other two consisting of agonistic and feeding behaviour. Comparison of the number of factors necessary to explain over 80% of the behavioural variance in warthogs with those for other species indicates that warthogs have a behavioural repertoire based on less complex causal relationships than primates, social carnivores and dolphins but more complex than that of bovines.

Introduction

Knowledge of warthog *Phacochoerus aethiopicus* behaviour has increased during the last 30 years, with qualitative descriptions having been given for warthogs in different areas of Africa (see Radke 1991 for a review and Somers 1992 for the present study area). They are therefore not repeated here.

To determine the role of various behaviour patterns in the social life of animals it is important to analyse their causal relationships (Rasa 1977). Both factor and concordance analysis are useful means by which behaviour patterns can be classified into those with similar causal relationships or similar motivational backgrounds and their comparison provides checks on the validity of the groupings found (Van Hooff 1970). The logic behind these types of analyses, which are based on behavioural sequences, is that the closer one behaviour pattern is related to another, the greater the tendency that each of them would be followed by other behaviour patterns in the behavioural repertoire at similar frequencies. These transition frequencies would thus be expected to show close correlation with one another. Factor analysis of the correlation coefficients obtained then allows their grouping into categories with a high degree of relatedness between behaviour patterns, as indicated by their high loadings on a particular factor. The relationship of a behaviour pattern with its highest loading on any one factor to those of other groups is indicated by its next highest and subsequent loadings on other factors discriminated by the analysis (Frey and Pimental 1978).

In this study on the causal factors of warthog behaviour, the frequency with which each behaviour pattern followed another was determined by sequence analysis. Warthog

behaviour patterns have not previously been analysed as to their causal factors. Since they are social group living animals a complex behavioural structure was predicted, as described for primates (van Hooff 1970) and social mongooses (Rasa 1977; Wenhold 1990).

Material and methods

The study was conducted on the Andries Vosloo Kudu Reserve (AVKR) ca 40 km north-east of Grahamstown, Eastern Cape Province, South Africa, between 33 × 04′ and 33 × 09′ S, and 26 × 37′ and 26 × 49′ E. For a description of the study area and animals used see Somers et al. (1995).

The data were collected from the central part of AVKR, the majority within a 1.5 km radius of a homestead (Grasslands). Observations were made from a vehicle, which served as a hide, and occasionally on foot. The warthogs which lived near Grasslands homestead were habituated to the presence of vehicles before the study began. Thirteen females and 34 males were individually known over the duration of the study period (March 1989–December 1990). Binoculars (7 × 35) were used when necessary. Groups were observed from the time they exited the burrows in the morning to the time they retired in the afternoon or evening.

To determine general activity (see Somers et al. 1995) scan samples (Altmann 1974) were taken at 5 min intervals for all visible members of a group (n = 887 hours). All occurrences of some events sampling were used especially for social behaviour patterns, which have a short duration and are likely to be under-represented in scans (Martin and Bateson 1993). If these occurred within the period of the 5 min scans, they were recorded in sequence.

The methods used for the sequence analysis were as previously described by Rasa (1977). The behaviour patterns included in this analysis were: resting, eating, retreating, standing, running, drinking, wallowing, grooming, allogrooming, suckling, greeting, playing (including solitary and social play), approaching, threatening, fighting, exiting of burrows, entering of burrows, excavation of burrows, scent marking, sniffing, grunting, squealing, courting and copulating, a total of 24. Walking was not included as nearly all behaviour patterns were necessarily correlated with it (Slater and Ollason 1972). As qualitative descriptions have been given elsewhere (see Radke 1991), only the descriptive names of behaviour patterns are given here.

Since a behaviour pattern could precede itself by a warthog stopping a particular behaviour at one site, walking to another and resuming that behaviour, the diagonal of the transition matrix was potentially full. Expected frequencies could therefore be calculated and these were corrected for random variation using the eccentricity coefficient (o-e)/(e, where o = observed frequency and e = expected frequency (Van Hooff 1970).

The eccentricity coefficients were then ranked and a Spearman's rank correlation analysis performed on the matrix, a particular behaviour pattern being considered as most closely correlated with itself and thus allocated the correlation coefficient "1.0". To determine communality amongst the behaviour patterns, the correlation coefficients were subjected to factor analysis with varimax rotation as well as concordance analysis using the method described by McQuitty (1966).

In the factor analysis four factors were extracted, these explaining 84.4% of the variance of all the behaviour patterns under consideration. Two behaviour patterns which loaded negatively on all four factors were considered separately.

Results

The first column of the factor analysis (Tab. 1) shows the highest loadings for different behaviour patterns on the four factors that explain 84,4% of the variance in warthog behaviour, 45.4% being explained by Factor I, 18.3% by Factor II, 12.6% by Factor III and 8.1% by Factor IV. The next highest loadings and the factors on which these loadings fall are shown in columns II–IV.

Those behaviour patterns with their highest loadings on a particular factor are grouped together (A, B, Ç, D). A further group (E), consisting of the, behaviour patterns

Table 1. A component analysis of the structure of behaviour patterns of warthogs, given by component loading (multiplied by 100). F = factor, L = loading

	Loading:	I (highest)		II (Second)		III (Third)		IV (Fourth)	
	Behaviour	F	L	F	L	F	L	F	L
A	Approach	I	74.5	II	48.5	III	39.6	IV	16.3
	Suckle	I	63.3	II	59.6	III	7.2	IV	0.2
	Exit	I	89.5	II	25.7	III	19.4	IV	16.2
	Threat	I	81.8	II	36.7	IV	27	III	–20.4
	Copulate	I	90.4	II	24.1	IV	17.6	III	17.1
	Squeal	I	75.4	III	43.3	II	41.6	IV	11.7
B	Retreat	II	91.2	I	10.8	III	3.9	IV	–25.9
	Greet	II	88.1	I	36.3	III	–4.6	IV	–15.2
	Court	II	65.0	I	51.8	III	14.3	IV	–4.6
	Play	II	14.9	III	0.5	I	–28.2	IV	–82.2
	Mark	II	24.5	III	11.8	IV	–7.8	I	–66.7
	Sniff	II	85.1	III	22.6	IV	17.8	I	3.9
C	Excavate	III	66.1	I	33.3	II	32.1	IV	–25.7
	Run	III	66.8	I	65.2	II	11.7	IV	8.0
	Wallow	III	70.8	I	55.8	III	19.3	IV	–24.3
	Allogroom	III	32.8	II	30.6	I	–7.1	IV	–88.3
	Rest	III	76.8	II	20.7	II	–30.1	I	–44.2
	Grunt	III	58.0	IV	55.3	II	42.7	I	26.7
	Groom	III	82.7	IV	23.3	II	11.2	I	–0.01
D	Fight	IV	74.4	III	50.8	I	22.4	II	21.7
	Enter	IV	52.3	III	44.9	I	17.3	II	–4.5
	Drink	IV	70.8	III	16.7	II	–10.9	I	–50.5
E	Eat	IV	–14.9	III	–21.5	II	–25.5	I	–90.3
	Stand	III	–18.7	II	–24.6	I	–53.3	IV	–71.8

"eat" and "stand", had negative loadings on all 4 factors, indicating that further factors are necessary to explain the complete behavioural repertoire.

Behaviour patterns of Group A, except for exiting of burrows, are social, as are all the behaviours in Group B. Groups C and D contained only one behaviour where interaction between two individuals occurred, namely allogrooming and fighting respectively. Group C contained behaviour patterns which can be broadly categorised as comfort behaviour, those of Group E being associated with feeding. The behaviour patterns falling into Group D, however, appear to have no common causal basis.

To determine the closeness of relationship between different behaviour patterns and to act as a check on the groupings extracted from the factor analysis, a concordance analysis was conducted using the correlation coefficients obtained from the transition matrices. The results are shown in Figure 1, the higher the concordance coefficient, the closer the causal relationship between behavioural complexes.

Six main groups were found to be present. The first one, A, corresponded to the first group from the factor analysis but included, in addition, courting and eating. Group A was further subdivided into three subgroups, the first including suckling, exiting and eating. This subgroup appeared to be hunger related. The second subgroup consisted of squealing and approaching, these being associated with initiation of social contact and the third subgroup included courting and copulating, sexually orientated behaviours. Group B comprised the behaviour patterns excavation of burrows and wallowing while Group C in-

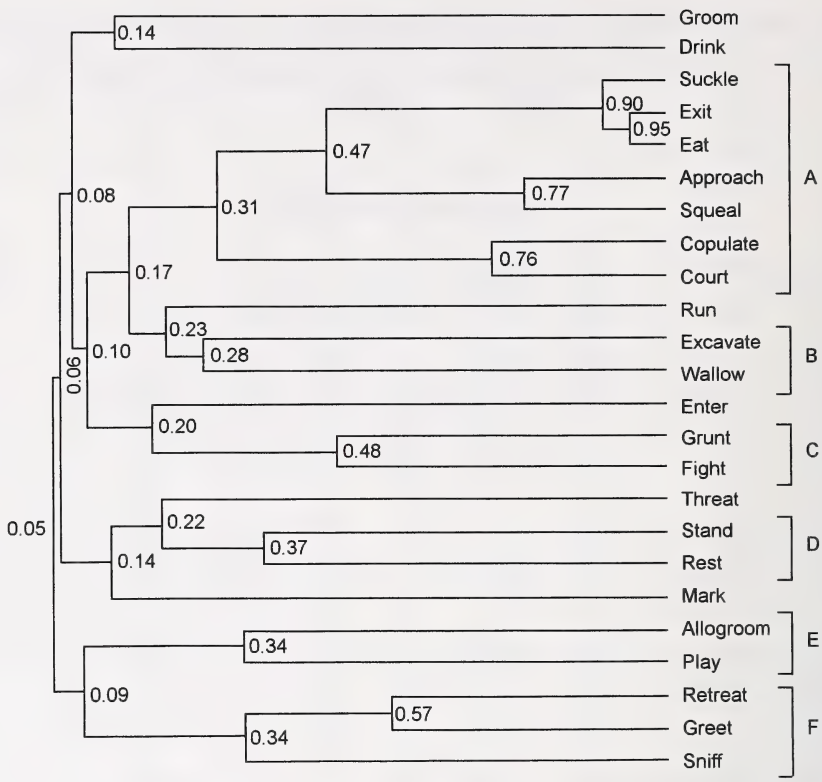


Fig. 1. Dendrogram of the relationships between behaviour patterns obtained through concordance analysis. The concordance coefficients are shown at the junction of the lines connecting the different behaviour patterns or behaviour pattern complexes.

cluded grunting and fighting, the latter being aggressive behaviour patterns. Group D consisted of standing and resting, both behaviours being associated with bodily inactivity. Group E contained allogrooming and play, behaviours occurring in a friendly social context while Group F was comprised of retreating, greeting and sniffing, these being associated with submissive behaviour.

The concordance analysis indicated that some behaviour patterns were not closely causally related to any others. The behaviour patterns concerned were grooming, drinking, running and entering of burrows, these being associated with body maintenance but causally unrelated. Threatening and marking, the other two behaviour patterns in this category, could both be loosely described as having an agonistic function.

Discussion

This study has shown that warthog behaviour can be subdivided into four main categories with a similar causal basis using factor analysis. Concordance analysis indicates that these relationships can be further subdivided into 8 categories with different motivational backgrounds, only 6 behaviour patterns showing no close causal association with any of the others. Five of these categories consist of behaviour patterns occurring in a social context, supporting the hypothesis that warthogs, being social, group-living animals, should show a high degree of behavioural complexity.

Of the subgroups with their highest loading on Factor I, those comprising Group B, burrow excavating and wallowing, are of especial interest since the findings suggest that burrow excavation has a function previously not recognised. During excavation, the soil is tossed into the air, covering the excavator and other warthogs in the vicinity. This may be a form of comfort behaviour, as is wallowing, soil being a protection against insolation and an aid in removing parasites, as in African elephants *Loxodonta africana* (Skinner and Smithers 1990). In the factor analysis wallowing and excavation of burrows have their highest loadings on the same factor as grooming and allogrooming, further supporting this hypothesis. The main function of burrow excavation was thought to be provision of a refuge for escape from predators (Bradley 1968, 1971; Cumming 1975; Radke 1985, 1991). Our data, however, indicate that it is more closely allied to comfort behaviour than to behaviour patterns associated with fleeing and escape or anti-predator behaviour (running, entering burrows or threatening).

Some groupings in both analyses may be explained by the fact that even if one activity always follows another, they may not be causally related to each other, but rather to some other factor (Staddon 1972). The results can be influenced by various factors such as the environment, and by individuals and groups differing (Slater and Ollason 1972). If the data from different animals are not combined, however, a massive quantity of data will have to be collected (Slater and Ollason 1972). These shortcomings in the data may explain the separation of behaviours which may otherwise be considered causally related. Entering and exiting burrows are weather and time dependent, entering occurring, for example, in the evenings and during the heat of the day. These external factors may have influenced both their factor loadings and concordance coefficients.

Van Hooff (1970) stated that, in sequence analyses, the less complex the behavioural structure, the smaller the number of components required to explain a large part (ca 70 to 80%) of the total variance. In warthogs, 84.4% of the variance was explained by only four factors, a fifth group being negatively loaded on these four. Comparison with other mammals indicates that 83% of behavioural variance is explained by 7 factors for chimpanzees, *Pan troglodytes* (Van Hooff 1970), 80% or more is explained by 11 factors for dwarf mongooses, *Helogale undulata* (Rasa 1977) and 81.5% is explained by 10 factors for yellow mongoose, *Cynictis penicillata* (Wenhold 1990). However, over 80% of the behaviour of captive silver (*Vulpes vulpes*) and blue (*Alopex lagopus*) foxes can be explained by 4 factors (Harri et al. 1995), by 5 for Hector's dolphin (*Cephalorhynchus hectori*), and only 3 for Holstein cows (de Passille et al. 1995). Warthog behavioural complexity therefore lies between that of the highly social primates and mongooses and the dolphins and at a level equivalent to foxes but above that of cattle.

Factor and concordance analyses are powerful tools for analysing causal relationships between behaviour patterns and are finding new application especially in the study of aberrant behaviour in domestic animals (Harri et al. 1995; de Passille et al. 1995). Probably owing to the difficulties inherent in conducting the analyses, those based on behavioural sequences are available only for a few species to date. This method of behavioural analysis, however, may also be useful in indicating phylogenetic relationships or levels of sociality for species, based on the number of factors necessary to explain behavioural variablity, as well as indicating causal relationships between behaviour patterns themselves.

Acknowledgements

Cape Nature Conservation is thanked for permission to conduct the research in the AVKR. Thanks for funding goes to the Foundation for Research Development, and the Eugene Marais Chair of Wildlife Management, University of Pretoria.

Zusammenfassung

Kausalanalyse der Beziehungen zwischen Verhaltensmustern freilebender Warzenschweine

Mittels Faktoren- und Konkordanzanalyse werden Kausalbeziehungen zwischen Verhaltensmustern freilebender Warzenschweine *Phacochoerus aethiopicus* im Andries-Vosloo-Kudureservat, Südafrika, untersucht. Die Ergebnisse weisen ein relativ unkompliziertes Verhaltensmuster auf. Die Aktivitäten sind allgemein in vier Gruppen verteilt, von denen soziale und andere Aktivitäten die zwei Hauptgruppen bilden.

References

ALTMANN, J. (1974): Observational study of behavior: sampling methods. Behaviour **49**, 227–267.

BRADLEY, R. M. (1968): Some aspects of the ecology of the warthog (*Phacochoerus aethiopicus* Pallas) in the Nairobi National Park. MSc thesis, Nairobi: University of Nairobi.

BRADLEY, R. M. (1971): Warthog (*Phacochoerus aethiopicus* Pallas) burrows in Nairobi National Park. E. Afr. Wildl. J. **9**, 149–152.

CUMMING, D. H. M. (1975): A field study of the ecology and behaviour of warthog. Mus. Mem. No. 7. Salisbury: National Museums and Monuments of Rhodesia.

DE PASSILLE, A.-M.; RUSHEN, J.; MARTIN, F. (1995): Interpreting the behaviour of calves in an open-field test: a factor analysis. Appl. Anim. Behav. Sci. **45**, 201–213.

FREY, D. F.; PIMENTAL, R. A. (1978): Principle components analysis and factor analysis. In: Quantitative Ethology. Ed. by P. W. COLGAN, New York: Wiley. Pp. 219–245.

HARRI, M.; REKILA, T.; MONONEN, J. (1995): Factor analysis of behavioural tests in farmed silver and blue foxes. Appl. Anim. Behav. Sci. **42**, 217–230.

MARTIN, P.; BATESON, P. (1993): Measuring behaviour: an introductory approach. Cambridge: Cambridge Univ. Press.

MCQUITTY, L. L. (1966): Similarity analysis by reciprocal pairs for discrete and continuous data. Educ. psychol. Measur. **26**, 825–831.

RADKE, R. (1985): Zur Ökologie und Ethologie des Warzenschweines (*P. aethiopicus*). Diplomarbeit, Berlin: Freie Universität Berlin.

RADKE, R. (1991): Monographie des Warzenschweines (*Phacochoerus aethiopicus*). Bongo (Berlin) **18**, 191–218.

RASA, O. A. E. (1977): The ethology and sociology of the dwarf mongoose (*Helogale undulata rufula*). Z. Tierpsychol. **43**, 337–406.

SKINNER, J. D.; SMITHERS, R. H. N. (1990): The mammals of the Southern African subregon. Pretoria: University of Pretoria.

SLATER, P. J. B.; OLLASON, J. C. (1972): The temporal pattern of behaviour in isolated male zebra finches: Transition analysis. Behaviour **42**, 248–269.

SLOOTEN, E. (1994): Behaviour of Hector's dolphin: classifying behaviour by sequence analysis. J. Mammalogy **75**, 956–964.

SOMERS, M. J. (1992): The implications of social structure for the conservation and control of a warthog *Phacochoerus aethiopicus* population in the Andries Vosloo Kudu Reserve, Eastern Cape Province. MSc (Wildlife Management) thesis, Pretoria: University of Pretoria.

SOMERS, M. J.; RASA, O. A. E.; PENZHORN, B. L. (1995): Group structure and social behaviour of warthogs *Phacochoerus aethiopicus*. Acta Theriol. **40**, 257–281.

STADDON, J. E. R. (1972): A note on the analysis of behavioural sequences in *Columba livia*. Anim. Behav. **20**, 284–292.

VAN HOOFF, , J. A. R. A. M. (1970): A component analysis of the structure of the social behaviour of a semi-captive chimpanzee group. Experientia **26**, 549–550.

WENHOLD, B. A. (1990): The ethology and social structure of the yellow mongoose, *Cynictis penicillata*. M. Sc. thesis, Pretoria: University of Pretoria.

Authors' addresses: M. J. SOMERS, Department of Zoology, University of Stellenbosch, 7600 Stellenbosch, South Africa and O. ANNE E. RASA, Abteilung Ethologie, Zoologisches Institut, Universität Bonn, Kirschallee 1, D-53115 Bonn, Germany.

Z. Säugetierkunde **62** (1997) 99–107

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Geographic variation and divergence in nonmetric cranial traits of *Arvicola* (Mammalia, Rodentia) in southwestern Europe

By J. Ventura and Maria A. Sans-Fuentes

Departament de Biologia Animal (Vertebrats), Universitat de Barcelona, Barcelona, Spain

Receipt of Ms. 00. 00. 1996
Acceptance of Ms. 00. 00. 1996

Abstract

Geographic variation and divergence of 21 nonmetric cranial traits were studied in six samples of water voles from southwestern Europe (*Arvicola terrestris*: southeastern and western Switzerland, French Massif Central, Spanish Pyrenees and northwestern Spain; *Arvicola sapidus*: Ebro Delta, Spain). Phenetic distance among samples was expressed by the mean measure of divergence (MMD) obtained from the transformation of the trait frequencies into angular values. From the MMDs of each sample, a cluster analysis was performed by the unweighted pair-group method using arithmetic averages (UPGMA). In the distance phenogram all samples of *A. terrestris* formed a cluster separated from *A. sapidus.* Among the former, the sample from southeastern Switzerland showed maximal phenetic differentiation against the remaining samples. The degree of phenetic divergence between the Iberian samples is higher than that between specimens from northwestern Spain and those from the Massif Central and western Switzerland. The lowest differentiation was observed between the samples from the Massif Central and western Switzerland. Since these results agree, in general terms, with our current understanding of the morphological, biometric, biochemical and reproductive relationships among several of the populations studied, nonmetric cranial traits can be considered useful for the evaluation of genetic differences in *Arvicola.* Under this assumption, taking into account the results obtained corresponding to the French and Spanish samples analysed, new considerations about the genetic relationships of central France, Pyrenean and northwestern Spain populations of *A. terrestris* are presented.

Introduction

Water voles of the Palaearctic genus *Arvicola* includes two species, which are recognised on the basis of morphological (Heim de Balsac and Guislain 1955), biometric (Reichstein 1963), cytogenetic (Matthey 1955, 1956; Díaz de la Guardia and Pretel 1979; Burgos et al. 1988) and biochemical characteristics (Graf and Scholl 1975; Graf 1982; Saucy et al. 1994): the southwestern water vole, *A. sapidus*, and the northern water vole, *A. terrestris.* The former is a semiaquatic rodent that occupies the Iberian Peninsula and much of France (cf. Reichstein 1982; Baudoin 1984). The northern water vole extends almost continuously throughout the northern Palaearctic region (cf. Corbet 1978) and shows two ecological forms: the fossorial and the semiaquatic (see e. g. Morel 1981). In southwestern Europe, where both species can be sympatric (Fig. 1), *A. terrestris* shows discontinuities in its distributional area (cf. Morel 1981; Baudoin 1984; Castién 1984; Álvarez et al. 1985; Ventura and Gosálbez 1988; Castién and Gosálbez 1993/94), which are associated with morphological, biometric and biochemical differences among several geographic populations (cf. Heim de Balsac and Guislain 1955; Reichstein 1963; Corbet et al. 1970; Engels 1975; Graf 1982; Ventura and Gosálbez 1989; Ventura 1991; Saucy et al. 1994).

Fig. 1. Geographic distribution of *Arvicola* in southwestern Europa (cf. Morel 1981; Baudoin 1984; Castién 1984; Álvarez et al. 1985; Ventura and Gosálbez 1988; Borghi et al. 1991; Castién and Gosálbez 1993/94). *A. sapidus*: horizontal lines; *A. terrestris*: vertical lines (fossorial form: widely spaced lines; semiaquatic form: densely spaced lines). Origin of the samples analysed: l: Lugano; 2: Nyon; 3: Ally; 4: Ribadesella; 5: Aran Valley; 6: Ebro Delta.

Variation in frequency of minor skeletal variants, known as nonmetric traits, are useful for assessing population variation in time and space as the result of genetic relationships (for theoretical considerations, see e.g. Howe and Parsons 1967; Berry and Jakobson 1975; Sjøvold 1977; Hauser and de Stefano 1989; McLellan and Finnegan 1990). In rodents, particularly, results obtained from the analysis of sets of nonmetric variants have been frequently used to evaluate genetic divergence among populations (e.g. Berry 1963; Berry and Searle 1963; Berry and Jakobson 1975; Patton et al. 1975; Berry et al. 1978; Hartman 1980; Sikorski 1982; Kryštufek 1990; McLellan and Finnegan 1990). To our knowledge only the study by Corbet et al. (1970) deals with the geographic variation of nonmetric characters in *Arvicola*; the incidence of nonmetric cranial traits in several European populations was used, together with biometric data, to elucidate the taxonomic status of British water voles.

The main goal of the present study is to determine the geographic variation of the frequencies of nonmetric cranial traits in several southwestern populations of *Arvicola*, and to evaluate the usefulness of these variants in systematic studies in this genus. A further aim of this study is to frame the genetic relationships among several Iberian and French populations of the northern water vole using nonmetric cranial variants. Although some of our specimens come from the same geographic regions as those surveyed by Corbet et al. (1970), we have grouped them differently, reflecting the taxonomic changes appearing after that study. Likewise, we have introduced further theoretical considerations established after the study by Corbet et al. (1970), to process nonmetric trait frequencies (cf. Green et al. 1979; Hartman 1980; Andersen and Wiig 1982).

Material and methods

The material analysed consisted of 259 skulls of adult specimens of *Arvicola* from the following six geographic samples, which are stored in the collection of the Department of Animal Biology (Vertebrates) at the University of Barcelona (Fig. 1): 33 from Lugano, Ticino, Switzerland (*A. t. italicus*), from July 1993; 21 from Nyon, Vaud, Switzerland (*A. t. scherman*), from June 1993; 60 from Ally, Massif Central, France (*A. t. scherman*), from July 1983; 54 from Ribadesella, Asturias, Spain (*A. t. cantabriae*), from July and August 1984; 55 from the Aran Valley, Lérida, Spanish Pyrenees (*A. t. monticola*), from July and August 1983; 36 from the Ebro Delta, Tarragona, Spain (*A. sapidus*), from 1983 and 1984. In contrast to the study by Corbet et al. (1970), we have grouped the individuals coming from the south (Lugano) and the north of the Alps (Nyon) in independent samples, since the semiaquatic animals from canton Ticino (Switzerland) show significant biochemical differences (Graf 1982) and mechanisms of reproductive isolation from the nearest fossorial populations from the north of the Alps (Morel 1981). Specimens from the Massif Central were also considered independently, in order to determine the degree of phenetic differentiation against the populations from Switzerland and Spain. Because of the significant biometric and morphological differences found between the Pyrenean (Aran Valley) and Cantabrian (Ribadesella) *A. terrestris* (Engels 1975; Ventura and Gosálbez 1989; Ventura 1991), specimens from those regions were also considered separately.

Twenty-one nonmetric traits were scored on the skull and mandible; sixteen were foramina and five were sutures or variations of the morphology of particular skull bones. All these characters were coded as discrete variables (present or absent; single or double). The following traits were considered (Fig. 2; definitions appear only in those traits not previously referred to in the literature or modified for *Arvicola* from other species): 1. Fused nasals; 2. Preorbital foramen double; 3. Anterior frontal foramen present; 4. Posterior frontal foramen double; 5. Frontal suture present: the posterior portion of the frontal suture is present; 6. Wormian bones present; 7. Interparietal bones not fused; 8. Foramen incisivum single; 9. Maxillary foramen I present; 10. Maxillary foramen II (lateral) present; 11. Palatal hollow: the posterior border of the palatine bone is bent forwards forming an arch; 12. Foramen sphenoidale laterale ventrale present; 13. Foramen sphenoidale medium present; 14. Basioccipital foramen present; 15. Foramen hypoglossi double; 16. Ethmoid foramen double; 17. Foramen ovale double; 18. Foramen infra-ovale absent; 19. Supra-dentary foramen present; 20. Mental foramen double; 21. Mandibular foramen double. All skulls used in this study were scored by the same person (MASF) in order to avoid inter-observer errors.

Several of the traits examined (2, 10, 12 and 21) showed more than two states (absent, single, double, triple, etc.). In order to obtain a simpler situation for comparative purposes (cf. Andersen and Wiig 1982), these particular traits were artificially dichotomized, and scored as absent or present (traits 10 and 12), or single or multiple (double, triple, etc.), in which case the trait was scored as double (traits 2 and 21). Since several skulls were damaged, the frequency of some traits was based on a lower number of specimens than the total sample size. Since every species possesses a characteristic set of minor skeletal traits (Sjøvold 1977), we used most of the variants examined in *Arvicola* by Corbet et al. (1970) and defined by Berry and Searle (1963; traits 2, 3, 4, 9, 10, 13, 14, 15, 17 and 20); likewise other variants used in other species (Bateman 1954: trait 8; Berry 1963: traits 12 and 21; Sikorski 1982: traits 1, 6, 7, 16 and 19) and other new variants for this genus (traits 5, 11 and 18) were analysed.

The percentage of occurrence of each trait was noted for all samples examined. Bilateral variants were scored on the right and left sides separately, and trait frequencies were calculated taking into account the total number of sides examined (for theoretical considerations, see Green et al. 1979). A nonmetric chi-squared test was used to evaluate the differences between sexes. Only those traits that differed significantly between at least two of the samples were used for comparative analyses (test $X^2 \geq 3.84$, $p \leq 0.05$; Andersen and Wiig 1982). In order to stabilize the variance (cf. Hartman 1980; McLellan and Finnegan 1990), the incidence of each character was transformed into angular values following Freeman and Tukey (1950; see also Sjøvold 1973; Green and Suchey 1976; Green et al. 1979). From these data, genetic differences between two samples were tested using C. A. B. Smith's mean measure of divergence (MMD), following Green et al. (1979). Statistical significance of the differences between two samples was tested by the standard deviation of MMD (Andersen and Wiig 1982; Sikorski 1982). The degree of divergence of one sample from the others was expressed by the measure of uniqueness (MU), which was calculated as the sum of the MMDs of each sample (Andersen and Wiig 1982). Based on the MMDs a phenogram was constructed by the unweighted pair-group method (UPGMA; Sneath and Sokal 1973) using arithmetical averages on the correlation matrix. A

phenogram was constructed using the routines SAHN and TREE of the Numerical Taxonomy System of Multivariate Statistical Programs (NTSYS-pc; Rohlf 1994).

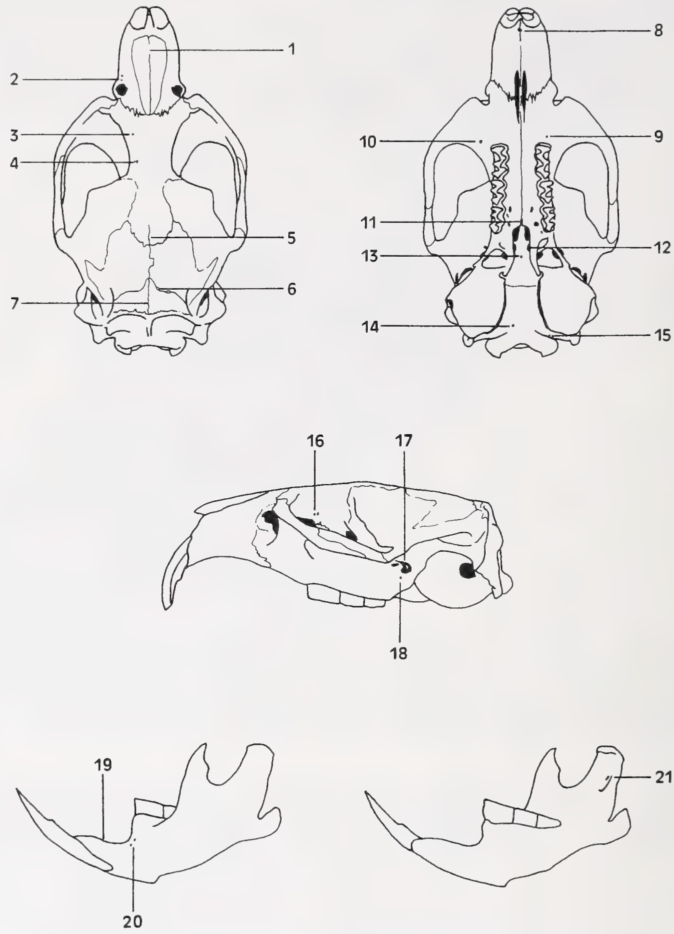


Fig. 2. Nonmetric cranial traits analysed in *Arvicola*.

Results

No significant difference between sexes was observed in the occurrence of cranial nonmetric traits in any sample, thus interpopulation analyses were performed using the combined frequencies for males and females (Tab. 1). Traits 15 and 19 did not differ significantly among samples. The frequent multiple division of trait 2 determined, in some cases, an arbitrary dichotomization of the character. Likewise, traits 1, 4 and 18 were sometimes very difficult to score. Comparisons of single trait incidence among samples indicated noticeable geographic variations in several cases, especially in traits 5, 8, 11, 13 and 21 (Tab. 1).

To compute phenetic divergence between pairs of samples the following 15 traits were considered: 3, 5–14, 16, 17, 20 and 21. The standard deviations of the MMDs obtained for these traits revealed that, except for the comparison between the samples from Nyon and Ally, all the phenetic distances among geographic samples were significant (Tab. 2). The

Table 1. Frequencies of 21 nonmetric cranial traits in six populations of *Arvicola* from southwestern Europe. *A. terrestris*: Lugano, Nyon, Ally, Ribadesella and Aran Valley; *A. sapidus*: Ebro Delta. k: trait occurrence; n: number of sides examined; %: percentage of trait occurrence.

Trait	Lugano		Nyon		Ally		Ribadesella		Aran Valley		Ebro Delta	
	k/n	%	k/n	%	k/n	%	k/n	%	k/n	%	k/n	%
1	27/33	81.8	19/21	90.5	47/56	83.9	9/47	19.1	46/54	85.2	23/35	65.7
2	7/64	10.9	7/41	17.1	28/107	26.2	52/96	54.2	8/106	7.5	8/71	11.3
3	1/66	1.5	2/41	4.9	13/93	14.0	11/92	12.0	6/110	5.4	2/72	2.8
4	5/66	7.6	6/42	14.3	6/75	8.0	11/94	11.7	0/110	0	0/72	0
5	18/33	54.5	3/21	14.3	5/48	10.4	2/50	4.0	0/55	0	5/36	13.9
6	0/66	0	0/42	0	2/89	2.2	1/98	1.0	0/110	0	9/69	13.0
7	0/33	0	0/21	0	2/48	4.2	0/49	0	0/55	0	5/36	13.9
8	11/33	33.3	14/21	66.7	42/60	70.0	39/48	81.2	43/54	79.6	19/36	52.8
9	30/66	45.4	14/42	33.3	31/115	27.0	20/97	20.6	38/110	34.5	35/72	48.6
10	41/65	63.1	37/42	88.1	97/111	87.4	85/98	86.7	92/110	83.6	70/72	97.2
11	29/33	87.9	18/21	85.7	32/58	55.2	23/52	44.2	51/55	92.7	24/36	66.7
12	46/57	80.7	39/42	92.9	44/57	77.2	71/87	81.6	61/106	57.5	70/70	100
13	8/33	24.2	1/21	4.8	2/39	5.1	20/48	41.7	4/55	7.3	36/36	100
14	0/66	0	1/42	2.4	11/84	13.1	8/98	8.2	19/110	17.3	15/72	20.8
15	65/66	98.5	40/42	95.2	85/85	100	98/98	100	109/110	99.1	71/71	100
16	10/66	15.1	1/42	2.4	1/87	1.1	0/96	0	6/110	5.4	4/72	5.6
17	66/66	100	41/42	97.6	77/81	95.1	93/96	96.9	108/109	99.1	65/72	90.3
18	29/65	44.6	34/40	85.0	49/79	62.0	54/95	56.8	47/109	43.1	45/67	67.2
19	0/66	0	0/42	0	0/120	0	1/108	0.9	0/109	0	0/71	0
20	8/65	12.3	9/42	21.4	9/120	7.5	13/108	12.0	1/109	0.9	0/71	0
21	35/66	53.0	10/41	24.4	41/105	39.0	41/103	39.8	22/109	20.2	6/71	8.4

highest MU value corresponded to *A. sapidus*, and, to a lesser extent, to the semiaquatic morphotype of *A. terrestris* from Lugano; the lowest MUs appeared in the fossorial populations of this latter species from Nyon, Ally and Ribadesella (Tab. 2). The phenogram of distances constructed from the MMDs matrix (Fig. 3) showed that the Ebro Delta sample (*A. sapidus*) appeared clearly separated from the samples of *A. terrestris*. Within these latter, the specimens from the south of the Alps differed significantly from the cluster formed by the remaining samples, in which the animals from the Aran Valley were the most different phenetically. The samples from Nyon and Ally formed a cluster that was significantly separated from the sample from Ribadesella.

Table 2. Mean Measures of Divergence (MMDs) in six populations of *Arvicola* based on the frequencies of 15 nonmetric cranial traits (upper matrix), and standard deviation for each MMD (lower matrix). For each sample the Measure of Uniqueness (MU) was calculated. *A. terrestris*: Lugano, Nyon, Ally, Ribadesella (Ribad.) and Aran Valley (Aran V.); *A. sapidus*: Ebro Delta (Ebro D.).

Sample	Lugano	Nyon	Ally	Ribad.	Aran V.	Ebro D.	MU
Lugano	–	0.1279	0.2383	0.3075	0.3304	0.6073	1.6114
Nyon	0.0198	–	0.0384	0.1105	0.1034	0.5365	0.9167
Ally	0.0132	0.0194	–	0.0530	0.1081	0.5522	0.9900
Ribad.	0.0130	0.0173	0.0106	–	0.1841	0.3917	1.0468
Aran V.	0.0124	0.0167	0.0101	0.0099	–	0.6463	1.3723
Ebro D.	0.0149	0.0192	0.0125	0.0123	0.0118	–	2.7340

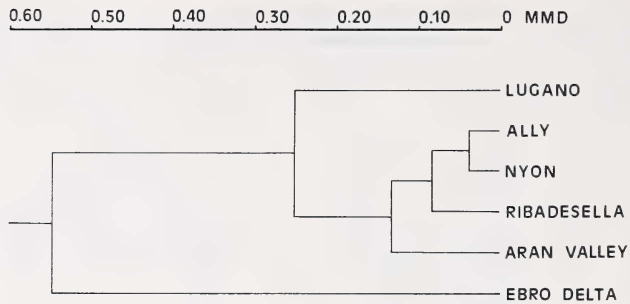


Fig. 3. Distance phenogram constructed from the MMDs obtained among six samples of *Arvicola* from southwestern Europe. *A. terrestris*: Lugano, Ally, Nyon, Ribadesella and Aran Valley; *A. sapidus*: Ebro Delta.

Discussion

The noticeable phenetic separation reported here between *A. sapidus* and *A. terrestris* coincides with the results given by Corbet et al. (1970), and thus the incidence of nonmetric cranial traits clearly agrees with the present taxonomic conception of the genus. Our results indicate that *A. sapidus* differs in general from all the samples of *A. terrestris* studied, and in particular, in the relatively high frequency of traits 6, 7 and 13, and the low incidence of trait 21. Comparing our data with the frequencies obtained by Corbet et al. (1970) for northern Spain *A. sapidus*, marked differences appear in traits 2, 4, 9 and 14. These differences are probably due to these traits being difficult to score objectively.

Among samples of *A. terrestris*, animals from Lugano are the most divergent in the incidence of nonmetric variants. These results are in accordance with the high genetic distance, deduced from gel electrophoresis data, between *A. t. italicus* and several semiaquatic and fossorial populations of the species (cf. Saucy et al. 1994) and, in particular, from the nearest fossorial populations of *A. t. scherman* from the north of the Alps (Graf 1982; Saucy et al. 1994). Based on the possible lack of gene flow between *italicus* and *scherman* (Graf 1982) and taking into account the mechanisms of reproductive isolation between them (Morel 1981), Graf (1982) suggested that both forms are on the way to becoming separate species. The high phenetic distance observed between our samples from Lugano and Nyon reaffirms the distinctiveness of *italicus* and *scherman*. In particular, from the variants used in the cluster analysis, the most conspicuous differences between the two forms appear in traits 5, 8, 10 and 21.

Although results of biochemical polymorphism have revealed a low level of genetic variability among fossorial populations of *A. terrestris* from southwestern Europe (Saucy et al. 1994), our results indicate significant variations among populations in the general incidence of nonmetric cranial traits. With respect to the data given by Corbet et al. (1970) for the specimens of *A. t. monticola* from the Pyrenees, our results corresponding to the sample from the Aran Valley also show noticeable differences in the frequencies of traits 4, 9 and 14, which might be due to the afore-mentioned subjective character of these variants.

Within the fossorial populations analysed, animals from western Switzerland and the Massif Central were phenetically similar, a result that coincides with their common subspecific status (cf. Morel 1981). On the other hand, both samples are more phenetically similar to the Cantabrian animals than to the Pyrenean ones. The general divergence in the incidence of the traits used in the comparative analyses (especially traits 11, 12 and 13) between animals from Cantabria and the Pyrenees support their different subspecific status (cf. Ventura and Gosálbez 1989; Ventura 1991).

The differences in frequencies of nonmetric cranial traits in southwestern European populations of *Arvicola* agree, in general, with our current understanding of the morphological, biometric, biochemical and reproductive relationships among several of these populations, and with their present taxonomic status. Therefore, we suggest that these traits can be considered useful for assessing genetic divergence among populations of this genus. Under this assumption, the results allow us to deduce new considerations on the genetic relationships between Iberian and French populations of *A. terrestris.* The significant phenetic divergences among the samples from the Pyrenees, Massif Central and northwestern Spain indicate the action of some barriers to gene flow. Available data on the geographic distribution of *A. terrestris* in France (cf. Baudoin 1984) and Spain (cf. Castién 1984; Álvarez et al. 1985; Ventura and Gosálbez 1988; Castién and Gosálbez 1993/94), suggest that the populations from the southwestern France departments of Lot and Garone, Gironde and Landes, and those from the Basque Country constitute fragmented groups of geographic populations (probably as shown in Fig. 1) representative of an earlier continuous distribution area, which connected the populations from the Cantabrian region, Pyrenees and southwestern and central France. The genetic drift accounts for at least some of the variability in nonmetric traits in both laboratory and wild populations (cf. Hartman 1980). Since population densities of the fossorial form of *A. terrestris* show multiannual fluctuations (cf. Saucy 1988), during troughs populations can pass through genetic bottlenecks, in which the genetic drift might especially act. This factor, together with the lack of gene flow because of geographic isolation, could have favoured the phenetic differentiation observed in the French and Spanish populations.

Acknowledgements

We are grateful to Dr. A. Meylan (Changins), Dr. E. L. Petavy (Lyon) and M. Braña (Oviedo) for the donation of the samples from Switzerland, the French Massif Central and Asturias, respectively. We thank Dr. J. B. Searle (York), Prof. Dr. J. Gosálbez and Dr. M. J. López-Fuster (Barcelona) for critical reading and constructive comments made on an earlier draft of this study. We also thank R. Rycroft (SAL, University of Barcelona) for improving the English text.

Zusammenfassung

Geographische Variation und Divergenz epigenetischer Schädelmerkmale bei Arvicola (Mammalia, Rodentia) in Südwesteuropa

Die geographische Variation und Divergenz von 21 nichtmetrischen Eigenschaften des Schädels wurde bei sechs *Arvicola*-Stichproben untersucht (*Arvicola terrestris*: Südosten und Westen der Schweiz, französisches Zentralmassiv, spanische Pyrenäen und Nordwesten Spaniens; *Arvicola sapidus*: Ebro Delta, Spanien). Die phänetische Distanz unter den Mustern wurde durch den mittleren Abweichungswert (MMD) ausgedrückt, der aus der Umwandlung der Charakterhäufigkeiten in Winkelwerte erhalten wurde. Ausgehend von den MMDs jedes Musters wurde mittels der UPGMA-Methode eine Gruppenanalyse erhoben. Im so erhaltenen Phänogramm der Abstände bildeten alle *A. terrestris* eine von *A. sapidus* getrennte Gruppe. In der ersten zeigte die Stichprobe aus dem Südosten der Schweiz die größte phänetische Abweichung gegenüber dem Rest der Gruppe. Innerhalb der iberischen Stichproben wurde ein größerer Grad an phänetischer Abweichung gemessen als zwischen den Exemplaren aus Nordwestspanien und denen aus dem Zentralmassiv und dem Westen der Schweiz. Die niedrigste Abweichung wurde zwischen den letztgenannten Stichproben beobachtet. Da die Resultate mit der allgemeinen Kenntnis über die morphologischen, biometrischen, biochemischen und reproduktiven Beziehungen zwischen den untersuchten Populationen übereinstimmen, kann man die nicht-metrischen Schädeleigenschaften als brauchbares Mittel zur Einschätzung der genetischen Differenzierung von Schermäusen und folglich zum Verständnis der phylogenetischen Beziehungen zwischen den Populatio-

nen bezeichnen. Unter dieser Annahme und in Anbetracht erhaltener Resultate können neue Hypothesen bezüglich der genetischen Beziehungen der Populationen im Zentrum Frankreichs, in den Pyrenäen und im Nordwesten Spaniens aufgestellt werden.

References

Álvarez, J.; Bea, A.; Faus, J. M.; Castién, E.; Mendiola, I. (1985): Atlas de los vertebrados continentales de Álava, Vizcaya y Guipúzcoa. Bilbao: Departamento de Política Territorial y Transportes, Viceconsejería del Medio Ambiente, Gobierno Vasco.

Andersen, T.; Wiig, O. (1982): Epigenetic variation in a fluctuating population of lemming (*Lemmus lemmus*) in Norway. J. Zool. (London) **197**, 391–404.

Bateman, N. (1954): Bone growth: a study of grey-lethal and microphtalmic mutants of the mouse. J. Anat. **88**, 212–262.

Baudoin, C. (1984): Le campagnol terrestre, *Arvicola terrestris*. In: Atlas des Mammifères sauvages de France. Ed. by M.-C. Saint-Girons and H. Maurin. Paris: Fayard. Pp. 164, 165.

Berry, R. J. (1963): Epigenetic polymorphism in wild populations of *Mus musculus*. Genet. Res. Camb. **4**, 193–220.

Berry, R. J.; Jakobson, M. E. (1975): Ecological genetics of an island population of the House mouse (*Mus musculus*). J. Zool. (London) **175**, 523–540.

Berry, R. J.; Jakobson, M. E.; Peters, J. (1978): The House mice of the Faroe Islands: a study in microdifferentiation. J. Zool. (London) **185**, 73–92.

Berry, R. J.; Searle, A. G. (1963): Epigenetic polymorphism of the rodent skeleton. Proc. Zool. Soc. London **140**, 557–615.

Borghi, C. E.; Martínez-Rica, J. P.; Giannoni, S. M. (1991): Quelques données nouvelles sur la distribution des rongeurs fouisseurs des Pyrénées d'Aragon (Espagne). Mammalia **55**, 445-447.

Burgos, M.; Jiménez, R.; Díaz de la Guardia, R. (1988): Comparative study of G- and C-banded chromosomes of five species of Microtidae: a chromosomal evolution analysis. Genome **30**, 540–546.

Castién, E. (1984): Contribución al estudio de la ecología y distribución de los micromamíferos de Álava, Guipúzcoa, Navarra y Vizcaya. Tesis de Licenciatura, Universidad de Santiago de Compostela.

Castién, E.; Gosálbez, J. (1993/94): Distribución de micromamíferos (Insectivora y Rodentia) en Navarra. Misc. Zool. **17**, 249–261.

Corbet, G. H. (1978): The Mammals of the Palaearctic region. London: Cornell Univ. Press.

Corbet, G. B.; Cummins, J.; Hedges, S. R.; Krzanowski, W. (1970): The taxonomic status of British Water voles, genus *Arvicola*. J. Zool. (London) **161**, 301–316.

Díaz de la Guardia, R.; Pretel, A. (1979): Comparative study of the karyotypes of two species of water vole: *Arvicola sapidus* and *Arvicola terrestris* (Rodentia, Microtinae). Caryologia **32**, 183–189.

Engels, H. (1975): Zur Kennzeichnung der spanischen Schermaus (*Arvicola terrestris monticola* de Sélys-Longchamps, 1838). Z. Säugetierkunde **40**, 372–377.

Freeman, M. F.; Tukey, J. W. (1950): Transformation related to the angular and square root. Ann. Math. Stat. **21**, 607–611.

Graf, J.-D. (1982): Génétique biochimique, zoogéographique et taxonomie des Arvicolidae (Mammalia, Rodentia). Revue suisse Zool. **89**, 749–787.

Graf, J.-D.; Scholl, A. (1975): Variations enzymatiques et relations phyletiques entre neuf espèces de Microtinae. (Mammalia, Rodentia). Revue suisse Zool. **82**, 681–687.

Green, R. F.; Suchey, J. M. (1976): The use of inverse sine transformations in the analysis of non-metric cranial data. Am. J. phys. Anthropol. **45**, 61–68.

Green, R. F.; Suchey, J. M.; Gokhale, D. V. (1979): The statistical treatment of correlated bilateral traits in the analysis of cranial material. Am. J. phys. Anthropol. **50**, 629–634.

Hartman, S. E. (1980): Geographic variation analysis of *Dipodomys ordii* using nonmetric cranial traits. J. Mammalogy **61**, 436–448.

Hauser, G.; de Stefano, G. F. (1989): Epigenetic variants of the Human Skull. Stuttgart: Schweizerbart.

Heim de Balsac, H.; Guislain, R. (1955): Evolution et spéciation des Campagnols du genre *Arvicola* en territoire Français. Mammalia **19**, 367–390.

Howe, W. L.; Parsons, P. A. (1967): Genotype and environment in the determination of minor skeletal variants and body weight in mice. J. Embryol. exp. Morph. **17**, 283–292.

Kryštufek, B. (1990): Nonmetric cranial variation and divergence of European sousliks (*Citellus citellus*) from Yugoslavia (Rodentia, Sciuridae). Boll. Zoll. **57**, 351–355.

Matthey, R. (1955): Nouveaux documents sur les chromosomes des Muridae. Problèmes de cytologie comparée et de taxonomie chez les Microtinae. Revue suisse Zool. **62**, 163–206.

Matthey, R. (1956): Nouveaux apports à la cytologie comparée des rongeurs. 7. *Arvicola amphibius amphibius* L. Chromosoma **7**, 670–692.

McLellan, L.; Finnegan, M. (1990): Geographic variation, asymmetry, and sexual dimorphism of nonmetric characters in the deer mouse (*Peromyscus maniculatus*). J. Mammalogy **71**, 524–533.

Morel, J. (1981): Le campagnol terrestre, *Arvicola terrestris* (L.), en Suisse: biologie et systématique (Mammalia, Rodentia). Thèse de doctorat, Université de Lausanne.

Patton, J. L.; Yang, S. Y.; Myers, P. (1975): Genetic and morphologic divergence among introduced rat populations (*Rattus rattus*) of the Galapagos Archipelago, Ecuador. Syst. Zool. **24**, 296–310.

Reichstein, H. (1963): Beitrag zur systematischen Gliederung des genus *Arvicola* Lacépède, 1799. Z. zool. Syst.-Evolut.forsch. **1**, 155–204.

Reichstein, H. (1982): Gattung *Arvicola* Lacépède, 1799 – Schermäuse. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. **2/I**, 209–252.

Rohlf, F. J. (1994): NTSYS-pc. Numerical Taxonomy and Multivariate Analysis System. New York: Exeter Publ.

Saucy, F. (1988): Dynamique de population, dispersion et organisation sociale de la forme fouisseuse du Campagnol terrestre (*Arvicola terrestris scherman* (Shaw), Mammalia, Rodentia). Thèse de doctorat, Université de Neuchâtel.

Saucy, F.; Wust Saucy, A.-G.; Pelz, H.-J. (1994): Biochemical polymorphism and genetic variability in aquatic and fossorial populations of the water vole, *Arvicola terrestris*, in western Europe. Pol. ecol. Stud. **20**, 559–573.

Sikorski, M. (1982): Non-metrical divergences of isolated populations of *Apodemus agrarius* in urban areas. Acta theriol. **27**, 169–180.

Sjøvold, T. (1973): The occurrence of minor non-metrical variants in the skeleton and their quantitative treatment for population comparisons. Homo **24**, 204–233.

Sjøvold, T. (1977): Non-metrical divergence between skeletal populations; the theoretical foundation and biological importance of C. A. B. Smith's mean measure of divergence. Ossa **4**, 1–133.

Sneath, P. H. A.; Sokal, R. R. (1973): Numerical Taxonomy. The principles and practice of numerical classification. San Francisco: W. H. Freeman and Company.

Ventura, J. (1991): Morphological characteristics of the molars of *Arvicola terrestris* (Rodentia, Arvicolidae) in its southwestern distribution area. Zool. Anz. **226**, 64–70.

Ventura, J.; Gosálbez, J. (1988): Revisión de la corología de *Arvicola terrestris* (Linnaeus, 1758) (Rodentia, Arvicolidae) en la Península Ibérica. Misc. Zool. **12**, 319–327.

Ventura, J.; Gosálbez, J. (1989): Taxonomic review of *Arvicola terrestris* (Linnaeus, 1758) (Rodentia, Arvicolidae) in the Iberian Peninsula. Bonn. zool. Beitr. **40**, 227–242.

Authors' address: Dr. Jacint Ventura and Maria Assumpció Sans-Fuentes, Departament de Biologia Animal (Vertebrats), Facultat de Biologia, Avgda. Diagonal 645, E-08028-Barcelona, Spain.

Z. Säugetierkunde **62** (1997) 108–116

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allozyme and isozyme variation in seven southern African Elephant-shrew species

By J. Raman and M. R. Perrin

Department of Zoology and Entomology, University of Natal, Scottsville, Natal, South Africa

Receipt of Ms. 16. 02. 1996
Acceptance of Ms. 20. 05. 1996

Abstract

Analysed were the allozyme and isozyme variation in seven species of southern African elephant-shrews. Allozyme and isozyme patterns obtained were species-specific. The data obtained showed a vast degree of divergence amongst the members of the genus *Elephantulus*, with Nei's genetic distance values ranging from 0.571 to 0.810 while the degree of divergence between *Macroscelides proboscideus* and *Petrodromus tetradactylus* was rather low, with a Nei's genetic distance value of 0.323. Genetic heterozygosity ranged from 0.000 to 0.055 while polymorphism ranged from 0.00% to 12.50%. Based on the results of UPGMA analysis *E. brachyrhynchus* was retained in the genus *Elephantulus*.

Introduction

Elephant-shrews are an order of small insectivorous mammals, endemic to Africa. Despite this restricted distribution, their classification both at the ordinal and species level has been the centre of much debate (Corbet 1978; Butler 1978, 1995). Earlier investigators have classified elephant-shrews as Tupaiidae, Hyracoidea and Lagomorpha (McKenna 1975; Tolliver et al. 1989). They have since been placed in an order of their own, Macroscelidea (Meester et al. 1986; Skinner and Smithers 1990).

The family, Macroscelididae, is divided into two subfamilies namely Rhynchocyoninae, which consists of one genus, *Rhynchocyon*, with three species and Macroscelidinae, comprising three genera namely, *Petrodromus*, *Macroscelides* and *Elephantulus* (Corbet and Hanks 1968). Both *Macroscelides* and *Petrodromus* include a single species whereas the genus *Elephantulus* comprises 15 species (Corbet 1974). Members of the Macroscelidinae, particularly those belonging to the genus *Elephantulus*, are widely distributed in Africa especially in the southern African subregion.

Subtle morphological differences in conjunction with biogeographical information has been used to delimit the different species of this genus. One *Elephantulus* species, *E. brachyrhynchus*, differs from the other members in this genus by having a third molar tooth on the lower jaw. Based on the possession of this feature, *E. brachyrhynchus* was initially placed in a genus of its own, *Nasilio*. The retention of the third molar tooth has since been identified as a primitive feature and therefore should not be used as the only feature to delimit genera (Corbet and Hanks 1968; Butler 1984). Using this argument *Nasilio* has been assigned to the genus *Elephantulus* (Corbet and Hanks 1968; Corbet 1974, 1995).

Most research involving these animals has been directed towards solving the ordinal question of these animals with very little research being conducted to either solve the tax-

onomy at the species level or to understand the biology of these animals. The research presented in this study forms part of a larger investigation aimed at understanding the biology and the evolutionary history of elephant-shrews. This portion of the study had three basic aims. The first aim was to assess the intra- and interspecific allozyme/isozyme variations of seven elephant-shrew species with the hope of identifying species-specific markers, second, it was hoped to establish on the basis of allozyme/isozyme analysis whether *E. brachyrhynchus* belongs to the genus *Elephantulus* or in a genus of its own. The final aim was to compare the phylogeny based on the allozyme/isozyme data with that based on morphological characters in order to assess which gave a clearer picture of the systematics and evolutionary history of these animals.

Material and methods

Animals

Seven southern African elephant-shrew species were investigated. The *Elephantulus* species (*brachyrhynchus*, *edwardii*, *intufi*, *myurus*, and *rupestris*) and *M. proboscideus* were trapped in Elliot small mammal traps while *P. tetradactylus* were caught in box traps previously used for trapping small carnivores. The localities at which the animals were trapped are shown in table 1. Once brought in from the field, the animals were treated for ectoparasites and housed in the departmental animal house in glass cages.

Table 1. Localities at which the elephant-shrew species were trapped.

Species	Area	Grid reference
E. brachyrhynchus	Princess Hill, Waterpoort, Northern Transvaal Province	20°54′ S 29°48′ E
E. edwardii	Nieuwoudtville, Northern Cape Province	31°23′ S 19°06′ E
E. intufi	Langjan Nature Reserve, Northern Transvaal Province	22°50′ S 29°15′ E
E. myurus	Deelfontein, Northern Cape Province	31°02′ S 23°46′ E
E. rupestris	Richmond, Northern Cape Province	31°10′ S 24°56′ E
M. proboscideus	Beaufort West, Western Cape Province	32°22′ S 22°33′ E
P. tetradactylus	False Bay, Kwazulu/Natal	27°57′ S 32°24′ E

Tissue homogenisation

Liver, kidney and heart tissue samples from individuals of each species were homogenised in an Optolabor ultra turrax (T25) at 0 °C. Liver and kidney samples were individually homogenised in phosphate buffered saline (pH 7,40) while heart samples were homogenised in 1,000 M KCl buffer. After homogenisation samples were centrifuged in a Beckman 200 E Microfuge (30 sec.; room temperature). Precipitates, containing cellular debris, were discarded while the supernatants containing active enzyme extracts were stored at 20 °C until needed.

Electrophoresis

Suitable dilutions of the enzyme extracts from each species were subjected to polyacrylamide gel electrophoresis using a Mighty Small SE 200 Electrophoresis unit. Polyacrylamide gels and electrode buffers were prepared according to the methods of either Hoefer (1993) or Krasfur (1993).

After electrophoresis, enzymatic activity was detected using various modifications of the stains suggested by Harris and Hopkinson (1978) and Selander et al. (1971). The enzymes tested for were: esterase 1 (ES 1; EC 3.1.1.1), esterase 2 (ES 2), esterase 3 (ES 3), fumarate hydrase 1 (FUM 1; EC 4.2.1.2), fumarate hydrase 2 (FUM 2), glucose dehydrogenase 1 (GD 1; EC 1.1.1.47), glucose-6-phosphate dehydrogenase 1 (G-6-PD 1; EC 1.1.1.49), glutamate oxaloacetate transaminase 1 (GOT 1; EC 2.6.1.10), glycerophosphate dehydrogenase 1 (GPD 1; EC 1.1.1.8), isocitrate dehydrogenase 1 (ICD 1; EC 1.1.1.42), isocitrate dehydrogenase 2 (ICD 2), lactate dehydrogenase 1 (LDH 1; EC 1.1.1.27), lactate dehydrogenase 2 (LDH 2), lactate dehydrogenase 3 (LDH 3), lactate dehydrogenase 4 (LDH 4), malate dehydrogenase 1 (MDH 1; EC 1.1.1.37), malate dehydrogenase 2 (MDH 2), malic enzyme 1 (ME 1; EC 1.1.1.40), mannose phosphate isomerase 1 (MPI 1; EC 5.3.1.8), phosphogluconate dehydrogenase 1 (PGD 1; EC 1.1.1.44), phosphogluconate dehydrogenase 2 (PGD 2), phosphoglucomutase 1 (PGM 1; EC 5.4.2.2), phosphoglucose isomerase 1 (PGI 1; EC 5.3.1.9), superoxide dismutase 1 (SOD 1; EC 1.15.1.1) and xathine dehydrogenase 1 (XDH 1). Staining of the polyacrylamide gels was achieved by using a solid substrate medium rather than the more commonly used liquid medium, as the former was found to be both more sensitive and more cost effective. The solid substrate medium was an agar gel (2%) containing substrate(s), essential cofactors and dye ingredients. The polyacrylamide gels were placed on top of a substrate gel and all the gels were incubated at 37 °C in the dark until bands appeared on the polyacrylamide gels (with the exception of esterases). For esterase staining Fast Blue Dye and naphthyl was added to agar. The polyacrylamide gels were then placed on top of the substrate gels, incubated at room temperature until satisfactory staining was attained. The stained polyacrylamide gel was then washed in fixative, fixed overnight and then the gels were dried on to filter paper and analysed. The stained polyacrylamide gels were then placed on to filter paper, air dried (24 h) and analysed.

Analysis of Data

The bands obtained on the polyacrylamide gels were initially termed electromorphs until a genetic basis for them was confirmed. Confirmation was achieved using the following procedure:

1) the number of bands detected in a heterozygous individual for each polymorphic locus was compared to known patterns of the enzyme in a polymorphic species e. g. man.
2) checks were made for known numbers of subunits for that enzyme in other species.

If these two criteria were met, then the electromorph was referred to as an allele. Alleles were coded according to their mobility from the origin with the most anodal allele coded "a" and successively more cathodal alleles as "b", "c" and so on until all the alleles were named. Adjacent comparisons of the alleles obtained from the enzyme extracts of the liver, heart and kidney tissues from individuals of the elephant shrew species were performed on all stains to ensure correct allelic designation. Statistical calculations were done using the BIOSYS 1 computer program of Swofford and Selander (1989).

Results

Results from tests for isozymes and allozymes from the three different tissue types (heart, liver, and kidney) from seven elephant-shrews species proved interesting. Although most of the loci tested displayed the same number of isozyme(s) and allozyme(s) in all three tissue extracts in all species e. g. MDH 1, occasionally the number of isozymes obtained in the different tissues varied e. g. LDH. The extracts of heart tissues tested for LDH activity, showed the presence of only three anionic isozymes while both the kidney and liver extracts showed the presence of all four anionic isozymes.

Statistical analysis of the allozymes and isozymes data was restricted to the data obtained from liver extracts, since this tissue produced the clearest and most reproducible

staining reactions for all loci tested. The allozymes and isozymes obtained from 26 presumptive loci are listed in table 2. Unfortunately the isozymes and allozymes for XDH could not be resolved in any of the tissue extracts tested, despite many various attempts at staining using different buffers and gel systems.

Table 2. Allelic designations of 23 genetic loci for seven elephant-shrew species.

LOCUS	SPECIES						
	*Eb**	*Ee**	*Ei**	*Em**	*Er**	*Mp**	*Pt**
ES 1	A	A	A	A	A	A	A
ES 2	A	A	A	A	A	A	A
ES 3	A	A	A	A	A	A	A
FUM 1	C	A	B	D	C	E	E
FUM 2	C	A	D	E	B	B	C
GD 1	**A**, D	C	B	C	C, **A**	E	E
G-6-PD 1	C	D	**B**, C	**B**, C	C	**A**, D	D
GOT 1	C	B	B	B	A	D	E
GPD 1	C	B	C	B	C	B	C
ICD 1	B	D	A	C	C	B	D
ICD 2	E	D	A	D	B	B, C	C
LDH 1	A	A	A	A	A	A	A
LDH 2	A	A	A	A	A	A	A
LDH 3	A	A	A	A	A	A	A
LDH 4	A	A	A	A	A	A	A
MDH 1	A	A	A	A	A	A	A
MDH 2	A	A	A	A	A	A	A
ME 1	C	C	A	C	B	C	C
MPI 1	B	A	D	C	E	C	C
PGD 1	A, **D**	A	B	C	D	D	D
PGD 2	D	C	A	B	B	E	E
PGM 1	B	A	C	B	C	C	A
PGI 1	B	A	B	B	A	C	C
SOD 1	B	A	B	B	A	C	C
SDH 1	D	C	A	B	A	F	E
XDH 1	–	–	–	–	–	–	–

**Eb – E. brachyrhynchus, Ee – E. edwardii, Ei – E. intufi, Em – E. myurus, Er – E. rupestris, Mp – M. proboscideus, Pt – P. tetradactylus.*
Bold alleles are the rarer forms found in the test sample.

Of the 26 loci examined, nine loci, LDH 1–4, MDH 1–2 and ES 1–3, were fixed in all the elephant-shrew species tested. Glucose dehydrogenase was found to be polymorphic in *E. brachyrhynchus* and *E. rupestris* while G-6-PD 1 was polymorphic in *E. brachyrhynchus*, *E. intufi*, *E. myurus*, and *M. proboscideus*. Only one individual from all the *E. brachyrhynchus* tested, possessed a different allele at the locus PGD 1 (Tab. 2) and one individual from all the *M. proboscideus* tested possessed a different allele at the locus ICD 2.

The degree of heterozygosity (H) was relatively low (Tab. 3), with the mean H varying from 0.000 in *P. tetradactylus* and *E. edwardii* to 0.055 in *E. brachyrhynchus* (Tab. 3). The H values of the other species tested were found in the midrange with *E. edwardii* possessing the lowest H (0.021) of this group. Like the degree of heterozygosity, the degree of polymorphism was relatively low, with *E. brachyrhynchus* showing the highest percentage polymorphism (12.50%) (Tab. 3).

Table 3. Mean heterozygosity (H) and percentage polymorphism (% P) in seven elephant-shrew species.

SPECIES	NUMBER OF INDIVIDUALS	% P	H ± SE
E. brachyrhynchus	10	12.50	0.055 ± 0.000
E. edwardii	10	0.00	0.000 ± 0.000
E. intufi	3	6.30	0.033 ± 0.033
E. myurus	10	6.30	0.021 ± 0.021
E. rupestris	10	6.30	0.032 ± 0.032
M. proboscideus	10	6.30	0.032 ± 0.032
P. tetradactylus	4	0.00	0.000 ± 0.000

The degree of similarity and difference between the species, using both Nei's (1978) genetic identity (I) and genetic distance (D) are shown in table 4. The values of D varied from 0.323 (between *M. proboscideus* and *P. tetradactylus*) to 0.970 (between *E. myurus* and *P. tetradactylus*). The values obtained using Nei's identity calculations produced a similar pattern to that of the distance values (Tab. 4). The D values between the *Elephantulus* species are quite large implying a high degree of divergence. The D value between *M. proboscideus* and *P. tetradactylus* is relatively low (0.323), implying a close relationship between these two species. The values obtained for Roger's (1972) genetic distance and genetic similarity calculations are shown in table 5. Although they mirrored the general

Table 4. Values of Nei's genetic identity (I, above the diagonal) and genetic distance (D, below the diagonal) between seven elephant-shrew species

SPECIES	*Eb**	*Ee**	*Ei**	*Em**	*Er**	*Mp**	*Pt**
*Eb**	–	0.469	0.473	0.464	0.511	0.465	0.469
*Ee**	0.756	–	0.445	0.505	0.483	0.406	0.500
*Ei**	0.749	0.810	–	0.553	0.474	0.388	0.381
*Em**	0.768	0.683	0.593	–	0.565	0.385	0.379
*Er**	0.671	0.728	0.747	0.571	–	0.516	0.445
*Mp**	0.765	0.9000	0.948	0.954	0.661	–	0.724
*Pt**	0.756	0.693	0.964	0.970	0.811	0.323	–

**Eb – E. brachyrhynchus, Ee – E. edwardii, Ei – E. intufi, Em – E. myurus, Er – E. rupestris, Mp – M. proboscideus, Pt – P. tetradactylus.*

Table 5. Values of Roger's genetic similarity (I, above the diagonal) and genetic distance (D, below the diagonal) between seven elephant-shrew species.

SPECIES	*Eb**	*Ee**	*Ei**	*Em**	*Er**	*Mp**	*Pt**
*Eb**	–	0.463	0.471	0.463	0.503	0.466	0.463
*Ee**	0.537	–	0.445	0.505	0.475	0.400	0.500
*Ei**	0.529	0.555	–	0.554	0.466	0.392	0.382
*Em**	0.537	0.495	0.446	–	0.550	0.389	0.380
*Er**	0.497	0.525	0.534	0.450	–	0.516	0.446
*Mp**	0.534	0.600	0.608	0.611	0.484	–	0.712
*Pt**	0.537	0.500	0.618	0.620	0.554	0.287	–

**Eb – E. brachyrhynchus, Ee – E. edwardii, Ei – E. intufi, Em – E. myurus, Er – E. rupestris, Mp – M. proboscideus, Pt – P. tetradactylus.*

pattern of the Nei values rather closely, they do not show as great a divergence amongst the species as predicated by the Nei's analysis.

Cluster analysis, employing the unpaired group method using the arithmetic mean analysis (UPGMA) of Nei's D and I values produced the phenograms shown in figures 1 and 2 respectively. Both phenograms divide the species into two main clusters which correspond to the *Elephantulus* and *Petrodromus/Macroscelides* groupings. The cluster containing *P. tetradactylus* and *M. proboscideus* appear to be far more closely related in terms of allozymic analysis, than initially thought. The *Elephantulus* grouping has *E. myurus* and *E. rupestris* the most closely related, with *E. edwardii* and *E. brachyrhynchus* the most divergent from this grouping (Figs. 1, 2).

The Wagner tree produced from the Roger's distance calculations, maintained the two broad genera clusters as shown by the Nei D and I calculations, but *E. brachyrhynchus* was classed within the *Macroscelides/Petrodromus* cluster (Fig. 3).

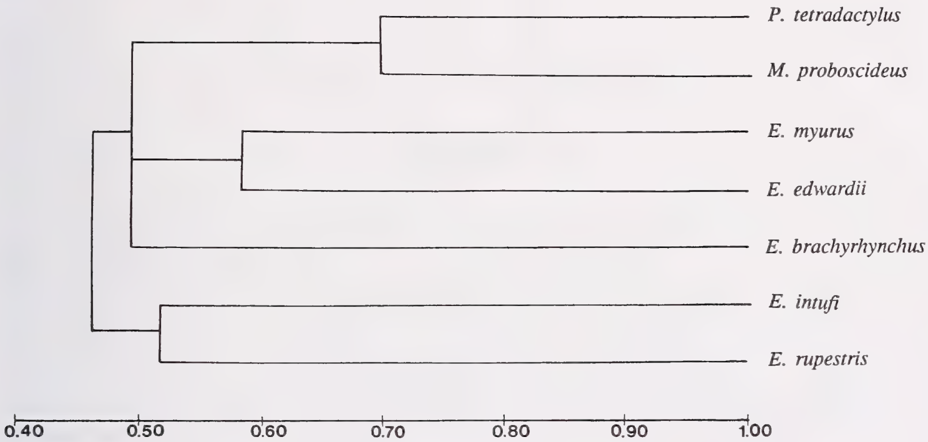


Fig. 1. Phenogram produced using UPGMA analysis of Nei's genetic identity of allozyme and isozyme data of seven elephant-shrew species (co-phenetic value = 0.864).

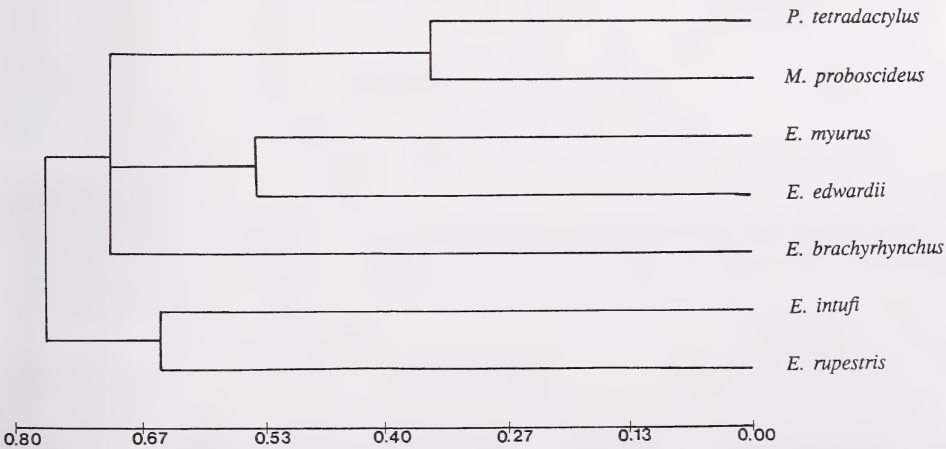


Fig. 2. Phenogram produced using UPGMA analysis of Nei's genetic distance for allozyme and isozyme data of seven elephant-shrew species (co-phenetic value = 0.820).

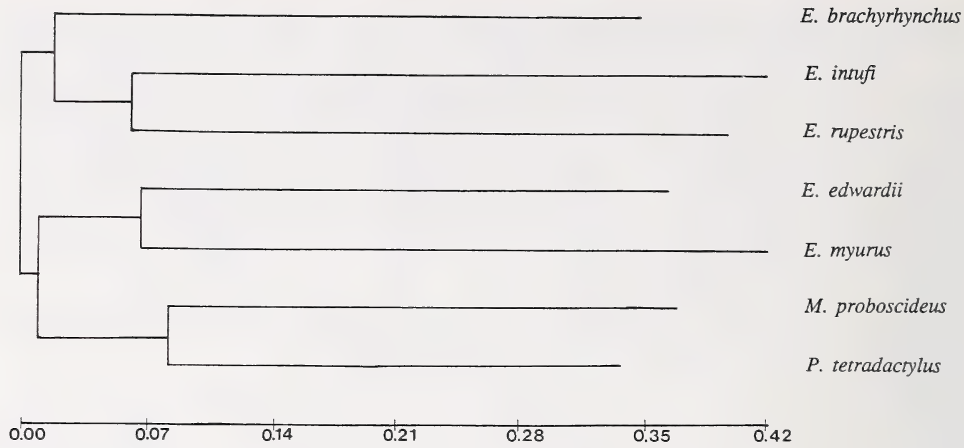


Fig. 3. Wagner tree produced using analysis of Roger's genetic distance of allozyme and isozyme data from seven elephant-shrew species (co-phenetic value = 0.818).

Discussion

When attempting allozyme analysis it is of vital importance to maintain and analyse different tissue extracts from each species, separately. Each tissue type has its own number and form of isozymes and allozymes and therefore when two different tissue types from the same species are mixed together, and subsequently analysed, the picture of isozyme and allozyme produced when subjected to electrophoresis is somewhat unclear, especially if they have different embryonic origins. Observed variations in the isozymes and allozymes patterns may be due to the differing concentrations of the tissues in the mixtures rather than due to real differences in the allozyme/isozyme patterns between different species. The mixing of tissues could be a possible reason for the discrepancy in the allelic results obtained by TOLLIVER et al. (1989) when compared to those of this study. TOLLIVER et al. (1989) used a mixture of two tissue types (heart and kidney) in their allozyme analysis of elephant-shrews and found more alleles per loci and a far greater degree of variation between the species.

In all the species sampled the percentage polymorphism and degree of heterozygosity was rather low. This could be due to the small sample size but it has been shown by GORMAN and RENZI (1979) as well as NEI (1978) that estimates of genetic distances obtained from data from a few animals do not vary significantly from those obtained from much larger sample sizes, providing a reasonable number of loci have been sampled.

The cluster/UPGMA tree produced from Nei's I values differed from the tree produced by TOLLIVER et al. (1989) as well as the dendrogram based on morphological features produced by CORBET and HANKS (1968). Unlike the trees produced in the previous studies, both *P. tetradactylus* and *M. proboscideus* appear to be closely related species rather than two distinct genera with I = 0.724 which is within the range for congeneric species suggested by AYALA (1975). Although the allozyme analysis suggests a close relationship, morphologically, behaviourally and chromosomally the two species are very distinct. Both of these species have very distinct habitats which do not overlap. These facts suggest that since these two species diverged from their common ancestor, selection pressure has been directed towards changes in morphology and behaviour patterns, making them better adapted to their specific environments rather than mutations occurring to prevent hybridisation between the two species. It is therefore suggested that these two species be maintained in two different genera.

The arrangement within the *Elephantulus* clustering using Nei's I values is interesting, with one of the most advanced species in this group being *E. myurus.*

Chromosomal analysis supports this, as the increase in this species's diploid chromosome number has been explained by the more advanced form of Robertsonian mutation, namely fission. Despite close morphological similarity between members of the genus, the Nei D and I values infer a great degree of genetic divergence between the species. A possible reason for this is that the morphological appearance adopted by the members of the *Elephantulus* cluster is the most evolutionary stable form for their general habitat and they have therefore diverged at the genetic level (chromosomes and allozymes) in order to prevent hybridisation.

Two basic clusters were also produced by the Wagner analysis of Roger's genetic distance but they differed from those produced by UPGMA analysis of Nei's genetic distance. In the Wagner analysis *E. edwardii* and *E. myurus* were classes with the *M. proboscideus* and *P. tretradactylus* grouping while *E. brachyrhynchus* was grouped with *E. intufi* and *E. rupestris.* This added credence to the argument that *E. brachyrhynchus* should be maintained in the genus *Elephantulus.* The accuracy of the genetic distance calculations and branch length estimates depends on the molecular clock hypothesis (Felsentein 1984) and many researchers are of the opinion that UPGMA analysis using Nei's genetic values best estimate the molecular clock. It is for this reason that the Wagner tree is disregarded. However, based on the UPGMA analysis of Nei's genetic distance and the fact that *E. brachyrhynchus* was maintained in the *Elephantulus* grouping by the Wagner analysis, it was decided to retain *E. brachyrhynchus* in the genus *Elephantulus* but as a species which had diverged from the common *Elephantulus* ancestor relatively early on in the development of this genus.

Allozyme analysis proved to be a good marker for the identification of different elephant-shrew species, since each species possessed its own unique allelic pattern. The allozyme analysis using Nei calculations also supported the general generic breakdown as well as the hypothesis that *E. brachyrhynchus* should remain within the *Elephantulus* genus rather than being placed in a separate genus. The phylogeny proposed by this study suggests that allozyme divergence within the elephant-shrew group has adopted two forms. The first occurs between the *Macroscelides* and *Petrodromus* genera, where the changes at the allozyme level have occurred more recently, most likely by genetic drift. The second occurs mainly in the *Elephantulus* taxon, where the allozyme divergence is primarily directed towards the prevention of hybridisation between the species.

Zusammenfassung

Allo- und Isoenzymvariation bei sieben Elefantenspitzmausarten des südlichen Afrika

Allo- und Isoenzymvariationsanalyse bei sieben Elefantenspitzmausarten aus dem südlichen Afrika zeigte in beiden Fällen artspezifische Muster. Die Auswertung, nach der Methode von Nei, ergab große Divergenz zwischen Angehörigen der Gattung *Elephantulus,* während sie zwischen den Arten *Macroscelides proboscideus* und *Petrodromus tetradactylus* gering war. Nach der UPMGA Analysemethode wurde *E. brachyrhynchus* als Mitglied der Gattung *Elephantulus* bestätigt.

References

Ayala, F. J. (1975): Genetic differentiation. Evol. Biol. **8**, 1–78.

Butler, P. M. (1978): Insectivora and chiroptera. In: Evolution of African mammals. Ed. by V. S. Maglio and H. B. S. Cooke. Cambridge, Mass.: Harvard Univ. Press.

Butler, P. M. (1995): Fossil Macroscelidea. Mammal Rev. **25**, 3–14.

Corbet, G. B. (1974): Family: Macroscelididea. In: The mammals of Africa: An identification manual. Ed by J. Meester and H. W. Setzer. Washington D.C.: Smithsonian Inc. Press.

Corbet, G. B. (1995): A cladistic look at classification within the subfamily Macroscelidinae based upon morphology. Mammal Rev. **25**, 15–18.

Corbet, G. B.; Hanks, J. (1968): A revision of the elephant shrews, family Macroscelididae. Bull. Brit. mus. Nat. Hist. (Zool) **16**, 47–111.

Felsentein, J. (1984): Distance methods for inferring phylogenies: a justification. Evolution **35**, 16–24.

Gorman, G. C.; Renzi, J. (1979): Genetic distance and heterozygosity estimates in electrophoretic studies: effect of sample size. Copeia **1979**, 242–249.

Harris, H.; Hopkinson, D. A. (1978): Handbook of enzyme electrophoresis in human genetics. Amsterdam: North Holland Publ. Co.

Hoefer Scientific Instrument Manual (1993): Basic techniques and exercise in electrophoresis. California.

Krafsur, E. S. (1993): Allozyme variation in stable flies (Diptera: Muscidae). Biochem. Genet. **31**, 231–240.

McKenna, M. C. (1975): Towards a phylogenetic classification of the mammals. In: Phylogeny of the primates: a multidisciplinary approach. Ed. by W. P. Luckett and S. Szalay. New York: Plenum Publ. Pp. 21–46.

Meester, J. A. J.; Rautenbach, I. L.; Dippenaar, N. J.; Baker, C. M. (1986): Classification of southern African mammals. Transvaal Mus. Monographs No 5. Pretoria: Transvaal Museum.

Nei, M. (1978): Estimates of average heterozygosity and genetic distance from small numbers of individuals. Genetics **89**, 583–590.

Rogers, J. S. (1972): Measures of genetic similarity and genetic distance. Studies in Genetics, Univ. Texas publ. **7213**, 145–153.

Selander, R. K.; Smith, M. H.; Yang, S. Y.; Johnson, W. E.; Gentry, J. B. (1971): Biochemical polymorphisms and systematics in the genus *Peromyscus*. I. Variation in old-field mouse (*Peromyscus polionotus*). Studies in Genetics IV, Univ. Texas publ.

Skinner, J. D.; Smithers, R. H. N. (1990): The mammals of the southern African subregion. Pretoria: Univ. Pretoria.

Swofford, D. L.; Selander, R. L. (1989): BIOSYS-1: A computer program for the analysis of allele variation in genetics. Urbana-Champaign: Univ. Illinois Press.

Tolliver, D. K.; Robbins, I. W.; Rautenbach, I. L.; Schlitter, D. A.; Coetzee, C. G. (1989): Biochemical systematics of elephant shrews from southern Africa. Biochem. Syst. Ecol. **17**, 345–355.

Authors' addresses: Jaishree Raman, and Prof. M. R. Perrin, Department of Zoology and Entomology, University of Natal, Private Bag X01, Scottsville, Natal, 3201, South Africa.

Z. Säugetierkunde **62** (1997) 117–118

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Observations of *Speothos venaticus* (Canidae: Carnivora) in its natural habitat in Peruvian Amazonia

By R. Aquino and P. Puertas

Instituto Veterinario de Investigaciones Tropicales y de Altura, Universidad Nacional Mayor de San Marcos, Iquitos, Peru

Receipt of Ms. 07. 06. 1996
Acceptance of Ms. 27. 09. 1996

The bush dog, *Speothos venaticus* (Lund, 1842) and the short-eared dog, *Atelocynus microtis* (Sclater, 1883), are the only representatives of the Family Canidae to inhabit tropical rainforest.

S. venaticus has a widespread distribution in neotropical forest (Linares 1968; Eisenberg 1989; Emmons 1990; Wozencraft 1993). Little is known about bush dog ecology and population dynamics since this species has seldom been observed in its natural habitat.

S. venaticus inhabits a wide range of forest types (Eisenberg 1989), but is never found far from a water course or forest cover (Peres 1991). Bush dogs usually live in small groups of four to seven individuals (Emmons 1990). These animals are thougt to be strictly carnivorous (Deutsch 1983; Peres 1991).

Here, we report the sightings of *S. venaticus* made in the Tamshiyacu-Tahuayo Communal Reserve and in the National Reserve of Pacaya-Samiria.

From July 1993 to September 1994, we sighted three groups of *Speothos venaticus*; two in the Tamshiyacu-Tahuayo Communal Reserve and one in the National Reserve of Pacaya-Samiria. In the first sighting, in July 1993, we observed two adults and an infant crossing a creek on a fallen tree trunk. We lost sight of the bush dogs once they had entered dense vegetation upon crossing the creek. The second sighting occurred in October 1993, at which time, a group composed of four individuals was observed for 15 minutes. Two adults explored a roughly circular area with a diameter of approximately 60 m. Their rapid and quiet movements were accompanied by a constant sniffing of the forest floor and of the undersides of fallen trunks. This activity was interrupted by abrupt pauses during which the ears were pricked each time a noise was heard. Normal activity was also interrupted on two occasions when the whining of an infant bush dog was heard. The whining was emitted from beneath a pile of branches in the center of the area of adult activity. When the whines of the infant ceased, the adults continued to explore the area. When the whine of the infant was heard again, the adults went to the pile of branches and reappeared a few seconds later, followed by juvenile and an infant. It is inferred that the infant had been left in the care of the juvenile while the parents foraged in the surrounding area. An adult, possibly the male, then led the group away. The infant, the last in the line, whined continously while following the other animals. The third sighting, on August 1994, occurred in the National Reserve of Pacaya-Samiria. Two adults and a juvenile were observed traveling in a line through "restinga". Having detected a human presence, the bush dogs froze and stared at the observers. They remained stationary for 35 seconds, until one adult set a urine scent mark. The group then moved away at moderate speed.

In addition to the three direct observations described, we found the carcass of an adult *S. venaticus*. The cause of death was indeterminable due to the advanced state of decomposition. It is possible that it had been killed by either *Felis concolor* or *Panthera onca*, since the tracks of a felid were abundant in the vicinity of the carcass.

We also found a den used by *S. venaticus*. The den was a large cavity in a fallen trunk. The walls of the cavity had been worn smooth, suggesting long term or frequent use as a den site. Both fresh and dried feces were found on one side of the trunk and in the surrounding area. The feces were examined in situ, and were found to contain mammalian hairs and avian feathers. The hairs of *Nasua nasua* and *Dasyprocta fuliginosa* were identified. Shorter hairs found may have belonged to *Myoprocta pratti* and *Proechimys* sp. The feathers were similar in colour to those of tinamous, terrestrial birds that are abundant in the area.

Following Encarnación's (1993) classification of forest types, the habitat of *S. venaticus* in the Tamshiyacu-Tahuayo Communal Reserve corresponds to "bosque de colina" and "bosque de terraza". However, the distribution of *S. venaticus* within these habitat types does not appear to be uniform, otherwise we should have encountered other groups of bush dogs during the intense exploration carried out in an area of more than 300 km^2. It is thus believed that the distribution of *S. venaticus* depends upon as yet undetermined factors acting at a local level.

Within "bajial" forest the bush dogs were encountered in forest of subtype termed "restinga" (Encarnación 1993). "Restinga" forest is seasonally flooded during the winter months. During this period, *S. venaticus* is thought either to retreat from the advancing waters or to remain isolated islands of higher ground in a manner similar to other sympatric terrestrial mammals (Bodmer 1990).

Acknowledgements

The authors would like to thank Suzi Leonard of the Detroit Zoo, Gesellschaft für Arten- und Populationsschutz, Munich and Gesellschaft für Primatologie, Göttingen for financial support of the studies in the Communal Tamshiyacu-Tahuayo Reserve. The manuscript was kindly translated by Christoph Knogge and Andrew Smith and benefitted from critical comments by Dr. Eckhard W. Heymann.

Literature

Bodmer, R. E. (1990): Responses of ungulates to seasonal indundations in the Amazon floodplain. J. Trop. Ecol. **6**, 191–201.

Deutsch, L. A. (1983): An encounter between a bush dog (*Speothos venaticus*) and paca (*Agouti paca*). J. Mammalogy **64**, 532–533.

Eisenberg, J. F. (1989): Mammals of the Neotropics. The northern Neotropics, Vol. 1. Panamá, Columbia, Venezuela, Guyana, Suriname, French Guiana. Chicago: Univ. Chicago Press.

Emmons, L. H. (1990): Neotropical Rainforest Mammals. A Field Guide. Chicago: Univ. Chicago Press.

Encarnación, F. (1993): El bosque y las formaciones vegetales en la llanura amazónica del Perú. Alma Mater **6**, 95–114.

Linares, O. J. (1968): El perro de monte. *Speothos venaticus* (Lund) en el norte de Venezuela (Canidae). Mem. Soc. Cient. Nat. La Salle **27**, 83–86.

Peres, C. A. (1991): Observation on hunting by small-eared (*Atelocynus microtis*) and bush dogs (*Speothos venaticus*) in central-western Amazonia. Mammalia **55**, 636–639.

Wozencraft, W. C. (1993): Orden Carnivora. In: Mammals Species of the World. A taxonomic and geographic reference. Ed. by D. E. Wilson and D. M. Reeder. Washington, D. C.: Smithsonian Inst. Press.

Author's address: Rolando Aquino Yarihuamán and Pablo Puertas Meléndez, Instituto Veterinario de Investigaciones Tropicales y de Altura, Universidad Nacional Mayor de San Marcos, Apartado 575, Iquitos, Perú.

Z. Säugetierkunde **62** (1997) 119–123

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Age determination of Iberian lynx (*Lynx pardinus*) using canine radiograph and cementum annuli enumeration

By Sonia C. Zapata, Rosa Garcia Perea, J. F. Beltran, P. Ferreras, and M. Delibes

Estación Biológica de Donana, Consejo Superior de Investigaciones Científicas, Sevilla, Spain and Museo Nacional de Ciencias Naturales, Consejo Superior de Investigaciones Científicas, Madrid, Spain.

Receipt of Ms. 06. 02. 1996
Acceptance of Ms. 04. 11. 1996

Age estimation of individuals is necessary to assess population dynamics and to help managers in the conservation of endangered populations (Johnston et al. 1987). Two methods are commonly used to determine the age of carnivores: counting of cementum annuli (CCA) and measurement of canine pulp cavity (CPC) (Grue and Jensen 1979; Johnston et al. 1987). The CCA method is based on the yearly addition of a layer of cementum on the outer surface of the tooth root (Johnston et al. 1987; Klevezal and Kleinenberg 1967). The CPC technique relies on the progressive accumulation of dentine in the pulp cavity, which tends to narrow with age (Johnston et al. 1987). The aim of the present study was to determine the feasibility of these complementary age techniques for the endangered Iberian lynx (*Lynx pardinus*). The age of closure of canine apical foramen will be also estimated.

We studied 89 Iberian lynx skulls from the collections of the Estación Biológica de Doñana, Seville, Spain, the Museo Nacional de Ciencias Naturales, Madrid, Spain, and the Natural History Museum, London, United Kingdom. Most of the specimens came from Doñana National Park (n = 58) (SW Spain), Sierra Morena (n = 10) (SW Spain), and Montes de Toledo (n = 21) (Central Spain). These three areas contain approximately 75% of the estimated total wild population of this species (Rodriguez and Delibes 1992). Dead specimens were found coincidently with ongoing studies; others were confiscated from poachers. The age of 7 individuals was known, based on registered birth dates (within a month) when radio-tracking after capture until their death. We also knew the minimum age of another sample of 14 individuals whose age was unknown at capture (although according to their weight 7 were yearlings and 7 were adults; see Beltran and Delibes 1993) and which were radio-tracked until their death. In order to estimate the age in months we assumed that all the individuals were born in April.

The lower left canine was extracted (after boiling mandibles) from 46 skulls (Tab. 1) and radiographed to measure pulp cavity at the point of its maximum width and canine diameter to the nearest 0.1 mm using a caliper. Then, we calculated the ratio of pulp cavity to canine width as a percentage. The open or closed condition of apical foramen was recorded for each extracted canine. Cementum annuli were counted on the third upper incisor (I^3) of 38 skulls. The incisors were decalcified in a 5% solution of nitric acid, sectioned at 20 μm thickness with a cryostat, and stained with Ehrlich hematoxylin (Klevezal and Kleinenberg 1967). We also analysed cementum annuli counts in 57 lower canines (prepared by Matson's Laboratory, Milltown, Montana). Enumeration of cementum annuli from canines and incisors of the same six animals were compared. Finally, we compared values of pulp cavity ratios with age estimates from counts of cementum an-

Table 1. Summary of methods applied for age determination and Iberian lynx specimens studied (n). Specimens include a sample of known-age individuals (known birth date +/–1 month), and minimum known-age individuals (age unknown when captured but radio tracked until death). Cemmentum annuli enumeration was performed in all the individuals, including the radiographed sample. I^3: only incisor, C: only canine, I^3 + C: incisor and canine.

	canine radiograph	cementum annuli count			n
		I^3	C	I^3 + C	
known age	4	5	0	2	7
minimum known age	8	11	0	3	14
unknown age	34	19	48	1	68
total	46	35	48	6	89

nuli. To determine whether there is an overlap between age-groups, pulp cavity data were plotted against annuli numbers, instead of relying on statistical tests which might be misleading (Johnston et al. 1987).

Our observations on canines from 18 lynxes aged 10 to 22 months (including 5 known-age specimens) indicated that a closure of the apical foramen occurs at an age of 12 to 18 months. Incremental cementum annuli were recorded in 67 specimens (Fig. 1). In the remaining 22 individuals, no fully formed annuli were observed. The counts of cementum annuli in canines and incisors of the same animal were in agreement. The number of complete cementum annuli ranged between 1 and 13. We examined tooth sections of specimens younger than 24 months with closed apical foramen to establish the age of the formation of the first cementum annulus. An annulus in process of formation was observed in six specimens aged 18 to 22 months, whereas one 18-month old specimen did

Fig. 1. Cementum annuli formed in a canine tooth of an Iberian lynx with a known age of 4 years from Doñana. Three annuli can be observed (1, 2 and 3).

not show any annulus. Similarly, a complete cementum annuli was observed in four specimens 24 months old (estimated age). Finally, one of two specimens 18 months old (known age) presented an annulus in process of formation, whereas there was no evidence of such a process in the other. In conclusion, the formation of the first complete cementum annuli probably starts around the 18th month of age, becoming apparent around the 22th month and being completed at about the 24th month of age. The formation period of this first complete annulus is from October to March.

An adult lynx (known age) born in spring 1985 and dying in August 1989 had three cementum annuli. On the other hand, all the 14 lynxes radio-tracked until their death had at least the minimum number of cementum annuli as expected from their known minimum age. These observations suggest that the formation of annuli occurs on a yearly basis. The oldest specimen of our sample was a male from Doñana. Its minimum age according to the radiotracking study was 7 years, but according to the enumeration of cementum annuli it was 14 years old.

The canine pulp cavity of two lynxes of known age 10 and 12 months was 73.3% and 60.9% of the canine width, respectively. In an 18-month specimen (known age) this percentage was 20.1%. In figure 2, the values of the canine pulp cavity ratios and the ages es-

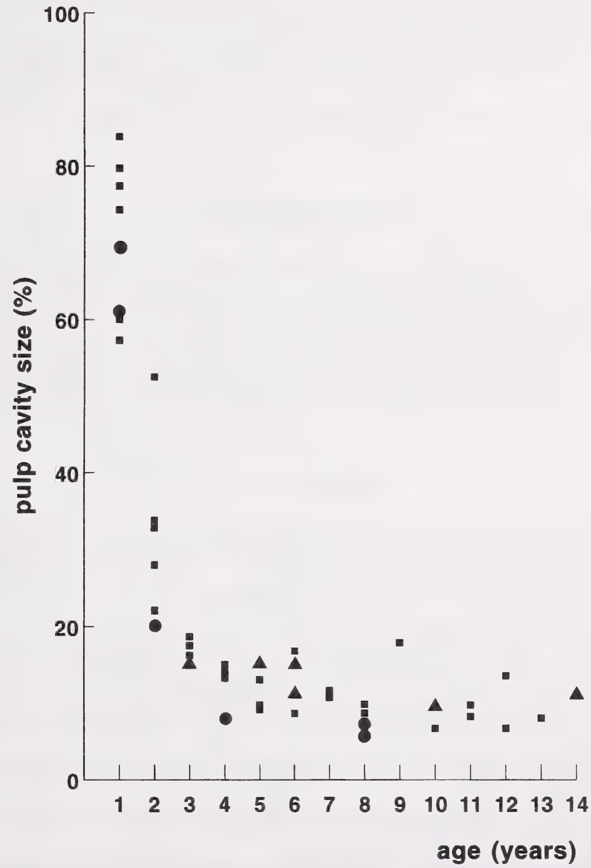


Fig. 2. Pulp cavity size expressed as a percentage of canine tooth width in relation to estimated age (cementum annuli) from our sample of Iberian lynxes. ■ lynxes with estimated age, ▲ lynxes with minimum known age and ● lynxes with known age.

timated by enumeration of cementum annuli are compared. The segregation of juveniles (less than 1 year and 1–2 years) from the remainder is clear, but it was not possible to separate age classes among the adults.

The time of closure of the canine apical foramen in the Iberian lynx agrees with published observations in bobcats (*Lynx rufus*) (CROWE 1972) and Canadian lynxes (*Lynx canadensis*) (BRAND and KEITH 1979). Nevertheless, in the Eurasian lynx (*Lynx lynx*) the complete closure of the apical foramen appears to occur at the 12th month of age (KVAM 1984). This criterion allows the separation of Iberian lynx juveniles from the other ages (see SAUNDERS 1963 and BRAND and KEITH 1979 for bobcat and Canadian lynx, respectively). Moreover, the method can be used on live anesthetized individuals via a simple radiograph of their canines. The canine pulp cavity width presents similar advantages. It appears to be adequate to separate juveniles from adults also in bobcats (JOHNSON et al. 1981), some canids (GRUE and JENSEN 1973, 1976) and some mustelids (JENKS et al. 1984; KUEHN and BERG 1981; DIX and STRICKLAND 1986).

The most accurate method for an age determination of adult Iberian lynxes in years is the enumeration of cementum annuli. The annual pattern of cementum deposition, as well as the period of formation of the first complete annulus, are similar to those detected by CROWE (1972) in the bobcat, by BRAND and KEITH (1979) in the Canadian lynx and by KVAM (1984) in the Eurasian lynx. Our observations on specimens of known-age confirm the reliability of estimating age in years by adding one to the number of complete cementum annuli. Some authors (BREITENMOSER et al. 1993) have estimated age of live-trapped individuals by counting the annuli of an incisor extracted from anesthetized Eurasian lynxes, with no apparent effects on the fitness of these individuals.

Acknowledgements

Funding was provided by Consejo Superior de Investgaciones Científicas (CSIC), and the Dirección General de Investigación Científica y Técnica (DGICYT) (projects PB87-0405, PB9O-1018 and PB92-0121); Consejería de Educación de Madrid (fellowship to R.G.P.); CSIC and Junta de Andalucía (fellowships to J.F.B.). We thank the Estación Biológica de Doñana (CSIC), the Museo Nacional de Ciencias Naturales (CSIC), and the British Museum of Natural History for permission to examine specimens in their collections. A. GREEN, J. A. DONÁZAR and CLAUDIA KELLER also contributed to improve the manuscript.

References

BELTRAN, J. F.; DELIBES, M. (1993): Physical characteristics of Iberian lynxes (*Lynx pardinus*) from Doñana, southwestern Spain. J. Mammalogy **74**, 852–862.

BRAND, C. J.; KEITH, L. B. (1979): Lynx demography during a snowshoe hare decline in Alberta. J. Wildl. Manage. **43**, 827–849.

BREITENMOSER, U.; KAVCZENKY, P.; DÖTTERER, M.; BREITENMOSER-WÜRSTEN, C.; CAPT, S.; BNERNHART, F.; LIBEREK, M. (1993): Spatial organization and recruitment of lynx (*Lynx lynx*) in a re-introduced population in the Swiss Jura Mountains. J. Zool. (London) **231**, 449–464.

CROWE, D. M. (1972): The presence of annuli in bobcat tooth cementum layers. J. Wildl. Manage. **36**, 1330–1332.

DIX, L. M.; STRICKLAND, M. (1986): Use of tooth radiographs to classify martens by sex and age. Wildl. Soc. Bull. **14**, 275–279.

GRUE, H.; JENSEN, B. (1973): Annular structures in canine tooth cementum in red foxes *Vulpes vulpes* of known age. Dan. Rev. Game. Biol. **8**, 1–2.

– (1976): Annual cementum structures in canines teeth of artic foxes (*Alopex lagopus*) from Greenland and Denmark. Dan. Rev. Game. Biol. **10**, 1–2.

– (1979): Review of the incremental lines formation in teeth and bones from mammals. Dan. Rev. Game. Biol. **11**, 1–48.

Jenks, A.; Bowyer, R. T.; Clark, A. G. (1984): Sex and age-class determination for fisher using radiographs of canine teeth. J. Wildl. Manage. **48**, 626–628.

Johnson, N. F.; Brown, B. A.; Bosomworth, J. C. (1981): Age and sex characteristics of bobcat canines and their use in population assessment. Wildl. Soc. Bull. **9**, 203–206.

Johnston, D. H.; Joachim, D. G.; Bachmann, P.; Kardong, K. V.; Stewart, R. A.; Dix, L. M.; Strickland, M. A.; Watt, I. D. (1987): Aging furbearers using tooth structure and biomarkers. In: Wild Furbearer Management and Conservation in North America. Ed by M. Novak, J. A. Baker, M. E. Obbard, and B. Malloch. Ontario, Canadá: Ministry of Natural Resources. Pp. 228–243.

Klevezal, G.A .; Kleinenberg, S. E. (1967): Age determination of mammals from annual layers in teeth and bones. Transl. 1969. Jerusalem: Israel Program for Scientific Translations.

Kuehn, D. W.; Berg, W. E. (1981): Use of radiographs to identify age-classes of fisher. J. Wildl. Manage. **45**, 1009–1010.

Kvam, T. (1984): Age determination in European lynx (*Lynx lynx*) by incremental lines in tooth cementum. Acta Zool. Fennica. **171**, 221–223.

Rodriguez, A.; Delibes, M. (1992): Current range and status of the iberian lynx *Felis pardina*, Temmnick 1824, in Spain. Biol. Conserv. **61**, 189–216.

Saunders, J. K. (1963): Movements and activities of the lynx in Newfoundland. J. Wildl. Manage. **27**, 390–400.

Authors' addresses: Sonia C. Zapata, J. F. Beltrán, P. Ferreras, and M. Delibes, Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apdo. 1056, E-41080 Sevilla, Spain; Rosa García-Perea, Museo Nacional de Ciencias Naturales Consejo Superior de Investigaciones Científicas, J. Gutiérrez Abascal 2, E-28006 Madrid, Spain.

Z. Säugetierkunde **62** (1997) 124–126

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allosuckling and daytime nursing pattern in farmed Red deer *Cervus elaphus*

By Gudrun Illmann, L. Bartoš, and J. Šiler

Research Institute of Animal Production, Praha, Czech Republic

Receipt of Ms. 05. 06. 1996
Acceptance of Ms. 29. 10. 1996

Allosuckling and adoption of young have been described for a number of social animals (Riedmann 1982; Packer et al. 1992). In farm animals, 'undesirable' adoption of young, 'mismothering', 'steeling' or 'poaching' of alien young are all terms used to describe these phenomena. They have been observed in sheep (Welch and Kilgour 1970) and cattle (Edwards and Broom 1982; Edwards 1983). Literature reports on mother behaviour in ungulates (Arman 1974; Alexander and Stevens 1982) describe repeated nursing and massaging the ano-genital region of an alien calf by a female as a possible indication of bonding. Nursing of their own and alien calves together by a female indicates probable parasitism of an alien offspring or cooperation between related individuals (Riedmann 1982; Packer et al. 1992; Birgersson et al. 1991). Kelly and Drew (1976) observed red deer in a farming situation. They observed calf sucklings of an alien hind to be very rare (2.7%), and were always quickly terminated when the hind paid no attention to the strange calf.

It is generally understood that allosuckling and adoption are more likely to occur when many pregnant females are living together around parturition, which is often the case on farms. Rare cases of allosuckling (Bubenik 1965) were also reported for free living red deer. Although mismothering in farmed red deer is common knowledge among farmers (Pemberton 1987), the development of this undesirable mother-alien calf bonding is not well understood.

The aim of this study was to determine (i) whether allosuckling occurs on the farm under observation, (ii) whether massaging the ano-genital region of an alien calf by a female could be regarded as a reliable indication that adoption had occurred, and finally (iii) whether there is a pattern to the time and/or frequency of day-time nursing.

The study took place in a 4 ha enclosure of a red deer *Cervus elaphus* farm at Vimperk, South Bohemia, Czech Republic, where 42 pregnant hinds with collars and 5 yearlings were kept. A total of 31 calves was born during the period of observation. Ten of them were collared within one day post partum.

The observations took place from a high seat in the centre of the enclosure. The observation was carried out between the 6th and the 28th of June from 6:00 to 21:00. Altogether the observation consisted of 152 hours, including four subsequent days of nearly continuous monitoring within the above-mentioned time range, during the peak period of activity. Each nursing event was recorded, together with the identity of the animals involved.

A total of 754 nursings of either one or more calves was recorded. Eight hinds nursed an alien calf in 18 different suckling events (2.4%). These hinds nursed the alien calf either alone (n = 11), or together with their own young (n = 7). Our results did not support Kelly and Drew's (1976) suggestion that in farmed red deer allosucking occurs

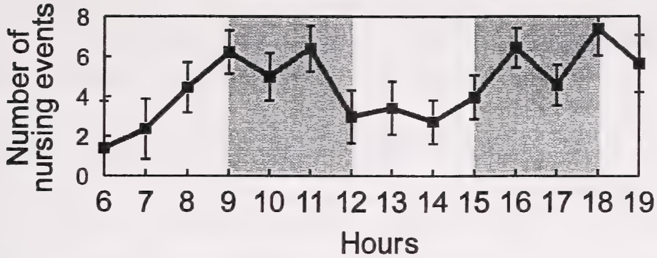


Fig. 1. The distribution of recorded nursings during the day is shown. The grey columne are selected periods for further investigation

when the deer are not accustomed to man. Although the incidence of allosuckling observed here was comparable to KELLY and DREW's (1976) results, the deer in this study were mostly tame. Our results, however, correspond well with reports on fallow deer (BIRGERSSON et al. 1991; BIRGERSSON and EKVALL 1994).

On 11 different occasions, four hinds licked the alien calfs ano-genital region during nursing. Two of these hinds nursed an alien calf only a few hours after giving birth. We had presumed that licking of the ano-genital region of the suckling calf by an alien hind indicated an adoption. To our surprise, however, two hinds were licking and massaging the ano-genital region of up to six different calves. Thus, to identify mismothering by a single observation of massaging the ano-genital region by an alien hind appears unreliable, and instead, detailed and continual observation over a long period is required.

Nursing data were subjected to the General Linear Models Procedure (GML) for Unbalanced ANOVA (SAS). Classes were 'Days' (17 days of observation) and 'Hours' (6:00 to 20:00). Least-squares means (LSMEAN) were calculated for each class and differences between classes were tested by t-test. The distribution of recorded sucklings during the day is shown in figure 1. The GML model was significant ($F_{(29,147)} = 2.03$, $P < 0.01$). While "days" of observation were very variable ($F_{(16,147)} = 2.32$, $P < 0.01$), the fluctuation of nursings during the day appeared almost non-significant ("hours" $F_{(13,147)} = 1.76$, $P = 0.06$). No precisely defined peaks of nursing activity were visible. For further investigation we selected the periods between 9:00 and 12:00 and between 15:00 and 19:00, which showed higher incidence of nursing. The high activity after 19:00 had to be omitted because of decreasing visibility due to approaching darkness. These selected periods covered most of the nursings observed (GLM model for selected and non selected periods $F_{(1,147)} = 8.24$, $P < 0.01$, figure 2). Our data on nursing activity agree with findings on the related fallow

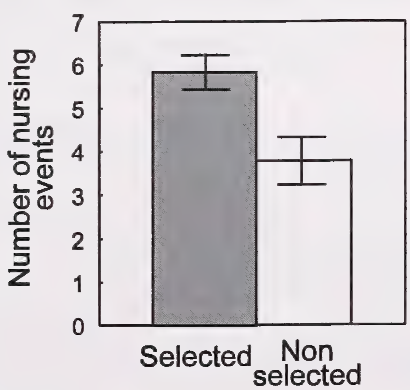


Fig. 2. Number of nursing events during selected and nonselected periods.

deer, where authors found no remarkable diurnal cycles of the nursing (Birgersson and Ekvall 1994). Kelly and Drew (1976) observed a pattern of nursing activity peaking in the early morning and evening and also with a higher incidence of nursing around 10.00 h, on red deer farm.

In conclusion, in contrast to our expectations, massaging of the ano-genital region of an alien calf by a female cannot be regarded as an indication of the establishment of a hind-calf bond in farmed red deer.

Acknowledgements

The authors wish to thank Jitka Lancingerová, Pavel Veverka, Hubert Herrmann, and Petr Janovsky for excellent field assistance and Arnošt Marks and Roberta Back for improving the English version. The project was supported by grants from the Ministry of Agriculture CR (AA 0930950139) and the Grant Agency of the Czech Republic (505/94/0639).

References

Alexander, G.; Stevens, D. (1982): Odour cues to maternal recognition of lambs: an investigation of some possible sources. Appl. Anim. Ethol. **9**, 165–175.

Arman, P. (1974): A note on parturition and maternal behaviour in captive red deer (*Cervus elaphus* L.). J. Reprod. Fert. **37**, 87–90.

Birgersson, B.; Ekvall, K. (1994): Suckling time and fawn growth in fallow deer (*Dama dama*). J. Zool. (London) **232**, 641–650.

Birgersson, B.; Ekvall, K.: Temrin, H. (1991): Allosuckling in fallow deer, *Dama-dama.* Anim. Behav. **42**, 326–327.

Bubenik, A. B. (1965): Beitrag zur Geburtskunde und zu den Mutter-Kind-Beziehungen des Reh- (*Capreolus capreolus* L.) und Rotwildes (*Cervus elaphus* L.). Z. Säugetierkunde **30**, 65–128.

Edwards, S. A. (1983): The behaviour of dairy cows and their newborn calves in individual or group housing. Appl. Anim. Ethol. **10**, 191–198.

Edwards, S. A.; Broom, D. M. (1982): Behavioural interactions of dairy cows with their newborn calves and the effects of parity. Anim. Behav. **30**, 525–535.

Kelly, R. W.; Drew, K. R. (1976): Shelter seeking and sucking behaviour of the red deer calf (*Cervus elaphus*) in a farmed situation. Appl. Anim. Ethol. **2**, 101–111.

Packer, C.; Lewis, S.; Pusey, A. (1992): A comparative analysis of nonoffspring nursing. Anim. Behav. **43**, 265–281.

Pemberton, J. M. (1987): Fallow genetics. The Deer Farmer. Dec., 17–20.

Riedmann, M. L. (1982): The evolution of alloparental care and adoption in mammals and birds. Quart. Rev. Biol. **57**, 405–435.

Welch, R. A. S.; Kilgour, R. (1970): Mismothering among Romneys. New Zealand Agriculture **121**, 26–27.

Authors' addresses: Dr. Gudrun Illmann, Dr. Luděk Bartoš, and Ing. Jiří Šiler, Ethology Group, Research Institute of Animal Production, CZ-104 Praha, Czech Republic

Z. Säugetierkunde **62** (1997) 127–128

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Buchbesprechungen

GANSLOSSER, U.; HODGES, J. K.; KAUMANNS, W. (eds.): **Research and Captive Propagation.** Fürth: Filander Verlag 1995. 338 pp., some illustrations and tables, paperback. 49,80 DM. ISBN 3-930831-01-5.

At first glance the title of this book is enigmatic: The general reader might ask questions as to what group of living beings the title refers: Plants or animals, invertebrates or vertebrates, anamniotes or amniotes, etc. lnspecting the book more closely, the reader learns that its contributions deal with birds and mammals in zoos.

After a short foreword by G. NOGGE, the President of the World Zoo Organisation, the table of contents lists 32 contributions authored by different researchers. This table lacks typographical differentiation and thus does not clearly show how the book is structured. According to the reviewer's impression there are six sections:

The editors give an introductory chapter on the scientific basis for animal management and conservation.

The following eight chapters deal with genetics, reproductive biology and technical problems of propagation of captive animals.

Four chepters deal with nutritional ecology, gastrointestinal anatomy, energetics and thermoregulation, as well as with Vitamin A and carotenoid metabolism.

Eleven chapters deal with behavioural aspects.

Breeding programmes in zoos, examples of biological research in these institutions and veterinary studies are presented in seven contributions.

Finally, two of the editors (W. KAUMANNS and U. GANSLOSSER) discuss – in an "evolutionary approach" – propagation in captive animals.

Most of the various contributions are followed by extensive lists of references. Some articles include tables or are illustrated. Diagrams and tables are clearly printed and easily legible, but half-tone illustrations, such as those on pages 50, 52 and 182 are practically worthless because of the very low quality of print!

In a book like the present one it is impossible to comment on all contributions. As is to be expected with a multi-authored book, the quality of the chapters is highly variable. Some articles present declamatory texts, and it has to be feared that they are just produced "for the files." However, the publication also includes interesting contributions concerning which the reviewer has chosen to make a few remarks.

C. P. GROVES emphasizes in his chapter that subspecies "can never be unscrambled" "once they have been mixed up". It is therefore necessary "to embark before it is too late on widespread taxonomic revisions of conservation-significant groups: what are the species, what are the subspecies, and how may they be distinguished?" (p. 28).

I. D. HUME discusses general concepts of nutrition and nutritional ecology and physiology. For the context of this book it is of great importance that the author emphasizes non-invasive and non-stressful experiments on nutrition and comparative physiology of animals in zoos. The reviewer believes that administrators of zoos should generally make their animals available to this type of experiments. This aspect is extended to natural history museums by K. LEUS and A. A. MACDONALD. These institutions must be encouraged to continue playing their traditional and vital role in the conservation of material for future research. C. WALZER and A. A. MACDONALD emphasize veterinary studies in zoos. The reviewer can only endorse the authors' statement that anatomists should be "responsible for the description of their species or group, ..." (p. 331), but he is sceptical that descriptive investigations by pathologists, as they are also recommended, can present more than post-mortem case histories of animals. This knowledge is important for the managers of the respective zoo, but it does not really extend our knowledge about basic information on the species.

E. MÜLLER presents a paper based on extensive studies of the energetics and thermoregulation in mammals and birds. From his results he is able to give recommendations on the thermal environment appropriate for species in captivity.

An interesting aspect is discussed in the study by C. HÖLZER et al. on the adaptation of captive-born

New Zealand takahes (*Porphyrio mantelli*) to non-captive life. The authors demonstrate that intensive training of "naive" birds to recognize their predator can be a promising approach before the animals are released.

For many non-specialist visitors elephants are probably the most important exhibit in zoos. F. Kurt and G. B. Hartl discuss Asian elephants (*Elephas maximus*); they deal with managment practices, characterize health and behavioural problems and present recommendations to cope with them.

P. Langer, Gießen

Kielan-Jaworowska, Z.; Gambaryan, P. P.: **Postcranial anatomy and habits of Asian multituberculate mammals**. Fossils and Strata No. **39**. Oslo, Kopenhagen, Stockholm: Scandinavian University Press 1994. 92 pp., 61 figs., 6 tabs. ISSN 0300-9491, ISBN 82-00-37650-8.

Multituberculata is an extinct group of mammals which endured from the late Jurassic (or even late Triassic if haramyiids are included) to the end of the Eocene, thus spanning a time period of 150 million years.

Multituberculates were the most diverse of Mesozoic mammals and their extinction during the Paleogene has been attributed to competition with herbivorous eutherians. Multituberculates have been placed in a separate subclass, the Allotheria, and currently there are several competing hypotheses of relationship to the three subclasses of extant mammals, monotremes, marsupials, and placentals. Although dental remains are rather common and diverse, postcranial bones are rare and mainly known of North American taxa.

The present study by two leading experts in Mesozoic mammals and mammal locomotion is based on a large number of postcranials of six Late Cretaceous multituberculate species from the Gobi Desert. The goal of the study is to describe in detail the skeletons and to reconstruct the musculature and habits of the animals. The minute size and the articulated condition of the fossils provide some drawbacks in this regard. The osteological descriptions of Part One of the monograph are well-complemented by photographs (mainly stereo-pairs) and clear line-drawings. A suite of new multituberculate autapomorphic and plesiomorphic characters is elaborated. The second part on muscular reconstructions looks somewhat tentative, as admitted by the authors themselves. Muscle attachments, in particular of smaller muscles, are in no way generally delimited by muscle scars or depressions on the bone. Multituberculates depart, on the other hand, in so many skeletal characters from therians that it appears highly speculative to transfer muscular arrangements of the latter to multituberculates in all details.

The following Parts Three and Four provide anatomical comparisons with other extant and fossil mammals and functional analyses, with an emphasis on locomotion and the multituberculate pes. Particular multituberculate features include: Cervical ribs, incipient supraspinous fossa and peg-like acromion, strongly twisted humerus, deep pelvis and large ilio-sacral angle, calcaneo-metatarsal V contact, and peculiar astragalonavicular articulation. The Late Cretaceous *Nemegtbaatar* is reconstructed with a rather sprawling stance and the authors conclude a digitigrade, terrestrial runner with an asymmetrical gait. The fore- and hindlimbs would have been abducted to some extent during locomotion.

Plesiomorphies and apomorphies of multituberculates are finally summarized and presumable habits and causes of extinction are discussed. Multituberculates are considered a sistergroup to all the other mammals. It is suggested that these Late Cretaceous Asian taxa were nocturnal semi-desert dwellers. Competitive inferiority to therians might has been related to the structure of the pelvis with a long ventral keel (short gestation period with extremely small neonates) and the abducted limbs (limited endurance for running long distances).

Multituberculates must have adapted to a variety of niches in their long-lived radiation while the present results are obtained from chronologically and geographically restricted samples. Another Cretaceous multituberculate from Mongolia, for example, was shown just recently to have possessed a forelimb like that of therians which was swung parasagittally and, moreover, some early Tertiary multituberculates from North America have been obviously arboreal. Nevertheless, this monograph will certainly become standard in vertebrate paleontology by the high quality of the analyses and the beautiful specimens described therein.

G. Storch, Frankfurt/M.

Instructions to Authors

Submission and Acceptance of Manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel, Germany, e-mail: dkruska@ifh.uni-kiel.de. Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by mail, and as soon as the peer reviews are received the authors will be informed concerning the decision for acceptance.

All correspondence dealing with details of production should be sent to: Zeitschrift für Säugetierkunde, Gustav Fischer Verlag, Villengang 2, D-07745 Jena, Germany.

Form of the Manuscript: Each manuscript should be submitted in triplicate, one original and two copies, in English or German in DIN A4 format either from a typewriter or legible computer print with a left-hand margin of 4 cm and true double spacing.

The first page of the manuscript should contain the following information:
title
name(s) of author(s): full first name for female authors, first initials only for male authors
department and university affiliation
In case of long titles, a running title not exceeding 72 characters should be provided.
Script type should be uniform throughout the manuscript. Use of bold print, italics and spaced-letters must be avoided.
Page footnotes and appendices at the end of the text are not allowed. Names of authors cited in the text are to be underlined in pencil. Botanical and zoological generic and species names should be underlined in pencil with a wavy line, whereby the name of the scientist who first described the species is not underlined.
Authors should indicate in the margins the approximate location in the text for illustrations and tables.
At the end of the manuscript following **References**, the exact postal address(es) of the author(s) should be given.

Content of the Manuscript: Manuscripts can be published as **original investigations** or **short communications.**

a) Original investigations: In addition to the text, original investigations should include illustrations, tables and references, and must not exceed 30 typewritten, double-spaced pages. The text should be divided into: Abstract (in English), Introduction, Material and methods, Results, Discussion (or together as Results and Discussion), Acknowledgements, Zusammenfassung (in German), References.

If written in German, an English title should precede the English abstract; if written in English, a German title should precede a German summary.

b) Short communications: Short communications must not exceed 5 typewritten, double-spaced pages and do not require either an Abstract or Summary. If written in German, an English title should be given on page 1; if written in English, please give a German title on page 1. Short communications need not be headed with subtitles into Introduction, Materials and methods, Results, and Discussion but should be organized according to this form.

Illustrations: Number and size of illustrations must be kept to an absolute minimum. Only well focussed and readily reproducible original prints showing optimal contrast can be accepted; colour plates cannot be processed. Labelling on figures should be uniform, and large and clear enough for eventual reduction in size. On the back of each illustration the following information should be given, using a soft pencil: figure number, name of the journal, first author. Captions to figures should be written on a separate sheet of paper.

Tables: The number and size of tables must be reduced to a minimum. Each table should appear on a separate page including heading and running number.

Comprehensive tables not fitting onto one page should follow on consecutive DIN A4 format sheets of paper.

References: Each paper cited in the text must appear in alphabetical order at the end of the text. Only internationally available literature should be quoted. The names of the journals should be given in abbreviated form in conformity to international use.

Examples
a) From journals:
Kalko, E. K. V; Handley, C. O. Jr. (1994): Evolution, biogeography, and description of a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá. Z. Säugetierkunde **59**, 257–273.
b) From books:
Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.
c) From reference books:
Niethammer, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

Printing: The principal author will receive page proofs of the manuscript as well as a set of the illustrations and the original manuscript for proof reading. Only type-setting errors should be corrected. Any major revision undertaken by the author at this stage will result in costs to the authors themselves. The conventional proof-readers' symbols should be used. The corrected page proofs should be signed by the author to indicate that the paper is "ready for print" and be sent to Prof. Dr. Peter Langer, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität Giessen, Aulweg 123, D-35385 Giessen, Germany, e-mail: peter.langer@anatomie.med.uni-giessen.de

Reprints: 50 reprints of each paper are supplied free of charge. When returning the page proofs additional reprints can be ordered at the cost of the author(s).

Publisher: Gustav Fischer Verlag GmbH & Co. KG, Branch Office Jena, P. O. Box No. 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/6 26-3; Fax ++49(0)36 41/62 65 00; e-mail: office.j@gfischer.de
Advertisement bookings: Enquiries should be directed to Gustav Fischer Verlag, Advertising Manager: Sabine Schröter, P. O. Box 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/62 64 28, Fax ++49(0)36 41/62 64 21
Advertising rates: The price list from October 1, 1994 is effective at present.
Distribution and subscription agency:
For customers **in the German speaking countries:** Please turn to your bookshop or to SFG-Servicecenter Fachverlage GmbH, Zeitschriftenvertrieb: Barbara Dressler, Villengang 2, D-07745 Jena, Germany. Phone ++49(0)36 41/62 64 44, Fax ++49(0)36 41/62 64 43;
For customers **in all other countries:** Please contact your bookshop or Stockton Press., c/o Debbie Floyd, The Subscription Dept., Houndmills, Basingstoke, Hants RG 21 6XS, UK. Phone ++44(0)12 56/5 18 98. Fax ++44/12 56/2 83 39. Subscribers in the **USA** can call toll free on ++1/800/747 3187.
Terms of delivery (1997): 1 volume consisting of 6 issues.
Subscription rate (1997): Price per volume: DM 398.00; ÖS 2 905.40; sFr 382.08; UK Sterling 183.00
Single issue price: DM 80.00; ÖS 584.00; sFr 76.80; UK Sterling 35.00
Reduced membership rates are available on request. Please turn to our publ. house.
All prices mentioned above are exclusive postage. USdollar prices are converted at the current exchange rate. We accept the following credit cards: VISA/Mastercard/American Express, (Please note card-No. and expiry date).
Banking connections:
For customers in the **German speaking countries:**
Deutsche Bank AG Jena, Konto-Nr. 6 284 707, BLZ 820 700 00.
For costumers **in the other countries:**
UK Post Office Giro Account No. 5 192 455. Full details must accompany the payment.
All prices are subject to change without notice.
Subsciption information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting, printing and binding: druckhaus köthen GmbH
Printed in Germany

Abstracted/Indexed in
Animal Breeding Abstracts; Current Contents Agriculture, Biology Environmental Sciences; Biological Abstracts; *BIOSIS* database; Current Advances in Ecological and Environmental Sciences; Dairy Science Abstracts; Fisheries Review; Helminthological Abstracts; Index Veterinarius; South Pacific Periodicals Index; Veterinary Bulletin; Key Word Index to Wildlife Research; Wild Review (Fort Collins); Zoological Record

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

DEUTSCHE GESELLSCHAFT FÜR SÄUGETIERKUNDE E.V. BERLIN

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Wissenschaftliche Kurzmitteilungen

GUSTAV FISCHER

ISSN 0044-3468
Z. Säugetierkunde
Jena · 62(1997)3 · S. 129-192
Juni 1997

3
1997

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **62** (1997) 129–142

ZEITSCHRIFT FÜR
SÄUGETIERKUNDE
INTERNATIONAL JOURNAL
OF MAMMALIAN BIOLOGY

Bat community patterns on the Accra Plains of Ghana, West Africa

By J. Decher

Bell Museum of Natural History, University of Minnesota, St. Paul, Minnesota, USA

Receipt of Ms. 02. 07. 1996
Acceptance of Ms. 28. 09. 1996

Abstract

Bat communities were sampled with mist nets at eight localities on the Accra Plains and two localities in the Northern Region of Ghana. I encountered five species of fruit bats (Pteropodidae) and 26 species from seven families of Microchiroptera in a total of 252 bats netted.

Glauconycteris poensis, *Hipposideros cyclops*, and *H. abae* were caught only in sacred groves protected by traditional law, whereas *Taphozous perforatus* was netted only near rocky cliffs in the legally protected Shai Hills Resource Reserve. *Myonycteris torquata* and *Myotis bocagei* were caught only at the edge of experimental forest plots in the northeastern part of the Accra Plains near the lower Volta River. There was a statistically significant negative correlation between canopy cover and bat species abundance and diversity.

Relatively open savanna at Shai Hills located close to bodies of water apparently had the greatest diversity and abundance of bats. The diversity of bats on the Accra Plains slightly exceeded published data from other savanna regions in West Africa.

Introduction

It is difficult to determine the "bat community" at any one locality because of the highly mobile nature of bats as compared to other mammals. The association of bat communities with certain plant communities may depend to some extend on the scale chosen; other variables such as presence of water may be more important. A large-scale study of bat communities in phytogeographic zones in Venezuela concluded that there was "little congruence between the floral zones as defined by phytogeographers and the bat species frequenting those zones" and that distribution of "riverine habitats and their associated faunas would tend to diminish the chance of detecting unique bat associations within phytogeographic zones" (Willig and Mares 1989). However, at each locality on the Accra Plains of Ghana it was obvious that a limited-time sample might yield considerable differences in abundance and diversity of bats, and that certain species seemed to be missing completely at some localities. Some species might also be absent during certain times of the year if they are seasonal migrants (Thomas 1983). The present study tested the null-hypothesis that bat communities on the Accra Plains are random assemblages at any given time and locality, versus the alternative hypothesis that bat communities are determined by various biotic and abiotic factors of the environment. Furthermore local bat diversity (= alpha diversity; Whittaker 1972) in Ghana is compared to local diversity calculated for bat communities of neighboring regions in West Africa.

The composition and distribution of bat communities on the Accra Plains of Ghana is not well known. Booth (1959) listed 6 species of fruit bats (Megachiroptera) and 12 insec-

tivorous species (Microchiroptera) with notes on distribution, habitat, and behavior, but did not mention the community structure of bats at the individual localities he mentioned.

There is also very little information on bat communities from elsewhere in Ghana. Marshall and McWilliams (1982) studied three species of epomophorine fruit-bats at Mole National Park in northern Ghana. Most studies to date have dealt with bats at the single-species level (McWilliams 1987, 1988, 1989) or with bat-plant interactions (Ayensu 1974; Baker and Harris 1957, 1959; Harris and Baker 1958, 1959; Lack 1978). Extensive unpublished collections of bats from Ghana, which include some specimens from localities on the Accra Plains, are housed at the British Museum of Natural History (BMNH), London; the Carnegie Museum of Natural History, Pittsburgh (CM); the Field Museum of Natural History (FMNH), Chicago; and the United States National Museum (USNM), Washington, D. C. There are also considerably fewer studies of syntopic bat assemblages from Africa than there are for the New World (Findley 1993). Three species of fruit bats (Pteropodidae) were studied in the Guinea savanna woodland at Lamto, Ivory Coast (Thomas 1982). A major early study of bat ecology was conducted by Verschuren (1957) at Garamba National Park in northeastern Zaire. Subsequently ecological studies were conducted in the Sengwa Wildlife Research Area in Zimbabwe (Fenton et al. 1977), in south-central Kenya (O'Shea and Vaughan 1980), in Lusaka, Zambia (Findley and Black 1983), and in part of Kruger National Park, South Africa (Aldridge and Rautenbach 1987).

Material and methods

During an eight-month study (November 1991 to June 1992; Decher 1996) of small mammal communities on the Accra Plains, bat communities were sampled in eight different habitat types. Two additional localities in the Northern Region of Ghana (Yendi and Bimbila) were sampled also and are included herein for comparison. Depending on topography, vegetation cover, and available time at each locality, I used from two to four mist nets of different sizes for one to four evenings in each habitat, once each during the dry and the early rainy season. Because of this unequal number of nets and sampling hours between habitats and sites, I have attempted to standardize efforts by using relative numbers caught and the proportion of bats caught per net night and net unit ($NN^{-1}NU^{-1}$) for the calculations presented. A net unit was defined as one 7-x-32-foot net (224 ft^2 = 20.8 m^2) resulting in a total of 141.7 net-nights for the study period. This standardization was based on the assumption that every net unit has an equal chance of catching each species of bat, which may not invariably be true, but between locality comparisons are considered to be valid because nets were placed to maximize diversity in all habitats and at each site. In dry forest, nets were set along narrow paths or perpendicular to the forest edge extending into the surrounding savanna. In the savanna, nets were stretched in presumed flyways, between savanna trees or, where possible, along the edge of water holes or ponds.

Localities on the Accra Plains (Fig. 1) can be characterized as follows:

1. Adumanya Sacred Grove (ASG): This grove was a 1.5 ha primary forest remnant at the foot of the Akwapim Escarpment on the northwestern edge of the Accra Plains, surrounded by farmland, mainly cassava (manioc) and maize. Three or four nets were set inside the grove perpendicular to each other.

2. Pinkwae Forest (PF): This site was a sacred forest that has been protected by the Ga people of Katamanso since the Ga-Ashanti war in 1826 (Lieberman 1979). Because of the thicket-like nature of this dry forest, three nets were set along narrow forest paths at each of two different sites inside the forest.

3. Kpong Fire Protection Site (KFPS): This site is a secondary forest on the more humid northeastern part of the Accra Plains, the result of savanna succession in a 0.75 ha plot protected from fire since 1957 (Carson and Abbiw 1990; Swaine et al. 1992). Two to four nets were set inside this forest and also perpendicular to the forest edge reaching into the surrounding grassland. In order to check for roof-dwelling species one net also was set apart from this forest near a guest house.

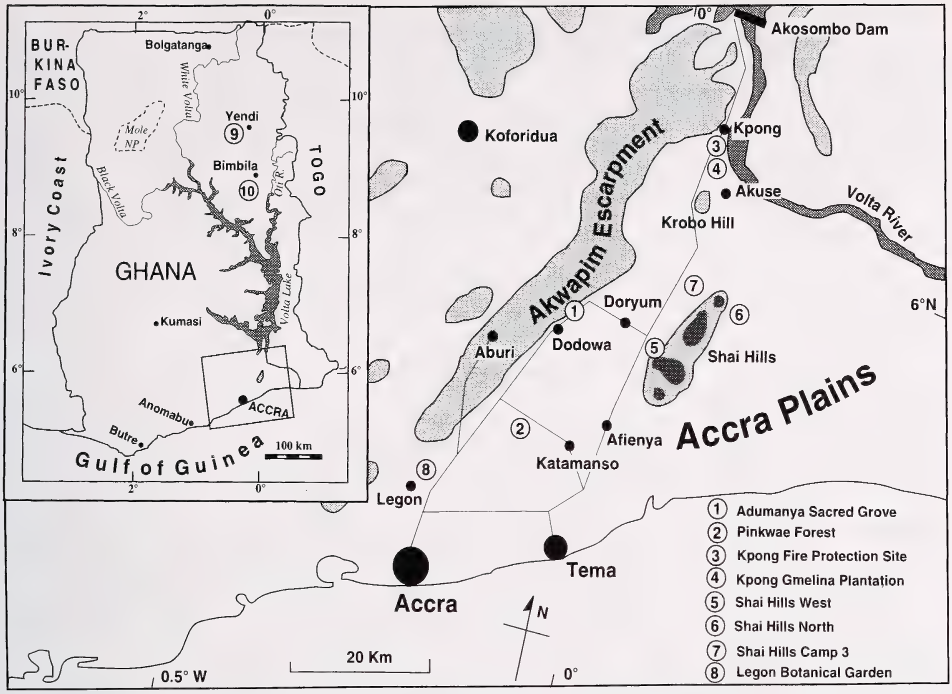


Fig. 1. Map showing 10 bat sampling localities on the Accra Plains and in Northern Ghana (insert).

4. Kpong *Gmelina* Plantation (KGP): Three nets were placed on paths inside this former plantation and perpendicular to the forest edge. This site was originally intended as a replicate for KFPS but will be treated separately because of its different vegetation history.

5. Shai Hills West (SHW): This site is located on the western slope of the Shai Hills Resource Reserve, a protected area enclosing an inselberg formation on the central Accra Plains. Three nets were set in various positions between savanna trees and in front of rocky cliffs.

6. Shai Hills North (SHN): This site is located in a "mosaic of *Vetiveria-Borassus* grassland and *Zanthoxylon-Capparis* thickets" (Schmitt and Adu-Nsiah 1993) in the north-east of Shai Hills Resource Reserve. Two to three nets were set along an artificial water hole bordered on three sides by thicket.

7. Shai Hills Camp 3 (SHC3): Two nets were set near this water hole located in the northwestern *Vetiveria-Brachiaria* grasslands of Shai Hills Resource Reserve for one day during the initial trial phase.

8. University of Ghana, Legon, Botanical Garden (LBG): Two nets were set at the edge of a pond at this locality for one night during the initial trial phase.

The two localities in the Guinea savanna of the Northern Region of Ghana, visited during the first month (November 1991; Fig. 1 insert), were as follows:

9. Yendi District Forestry Station (YEN): Two mist nets were tended for one evening on 1 November 1991 in the garden of the Forestry Station (9°25′ N, 0°04′ W).

10. Bimbila Reservoir (BIM): Two nets were set here at the edge of a water hole (3.5 km west of Bimbila; 8°52′ N, 0°02′ E) during evening hours of 4 November 1991.

I calculated Simpson's Index of diversity ($D = \Sigma p^2$), expressed as 1-D, defined as the probability of picking two individuals that are different species. I also calculated the Shannon-Wiener function of diversity ($H' = -\Sigma(p)(\log_2 p)$), the number of equally common species with the same diversity as H' ($N1 = e^{H'}$), and the evenness index $J' = H'/H'_{Max}$ (Krebs 1989). These diversity indices and the number of species netted were then compared to map measurements of distance to open water, distance to nearest forested hillside or escarpment, and tree canopy closure at the site using the SAS procedure for Pearson's correlation coefficient, PROC CORR (SAS Institute 1982). The choice of these variables

Table 1. Summary of bats sampled on the Accra Plains (1991–92) and at Yendi and Bimbila in northern Ghana (Nov. 1991). See text for abbreviations.

	Locality										Tot.
	ASG	PF	KFPS	KGP	SHW	SHN	SHC3	LBG	YEN	BIM	
No. of Nights (NN) netted:	4	8	4	2	6	6	1	1	1	1	34
Net Units (NU)[a]:	5.3	3.8	4.3	4.8	4.1	4 .4	4.6	4.6	2.9	4.6	
Species											
MEGACHIROPTERA											
Eidolon helvum[b]	>1000										
Epomophorus gambianus				1			1	9	1	3	15
Epomops franqueti	1		2								3
Micropteropus pusillus	1	3	6	4	20	9	1		1		45
Myonycteris torquata			2								2
MICROCHIROPTERA											
Eptesicus capensis						1	3				4
Eptesicus guineensis					1	2		1	1		5
Eptesicus rendalli						3					3
Glauconycteris poensis	2										2
Glauconycteris variegata						2					2
Hipposideros abae		2									2
Hipposideros beatus						12					12
Hipposideros commersoni						5	1				6
Hipposideros cyclops	4										4
Hipposideros ruber				2		3			1		6
Lavia frons					1	6					7
Myotis bocagei				1							1
Nycteris hispida		3		1′		5					9
Nycteris macrotis		10	3	1	2						16
Nycticeinops schlieffenei						1					1
Pipistrellus aegyptiacus						1					1
Pipistrellus nanulus						5					5
Rhinolophus landeri		1		3	3	2					9
Scotoecus albofuscus						4					4
Scotophilus dinganii					2			3			5
Scotophilus leucogaster									2		2
Scotophilus viridis nigritellus					2	10	1				13
Tadarida condylura[c]			52								2
Tadarida nigeriae										12	12
Tadarida pumila									2		2
Taphozous perforatus					2						2
Total individuals per Habitat:	8	19	13	13	33	71	7	13	8	15	252
Total No. of Species:	5	5	5	7	8	16	5	3	6	2	31

[a] one net unit = one 7 × 32 ft net = 224 ft^2 (20.8 m^2)
[b] *Eidolon helvum* numbers in the canopy of Adumanya Sacred Grove Canopy were estimated at > 1 000 individuals and have been excluded from totals.
[c] *Tadarida condylura* was excluded from totals because this species was caught emerging from a building at Kpong Agricultural Research Station (most of the 52 individuals caught were released).

was based on the assumptions that many species of bats are attracted to water for drinking and for hunting insects, forested hillsides and rock outcrop provide better opportunities than the open grasslands for finding roosting places for most species, and dense vegetation and a closed canopy create conditions better suitable for complex "syntopic assemblages of bats" (FINDLEY 1993). For a tentative functional analysis of community structure, I grouped the bat species sampled in each habitat into foraging-trophic groups as defined by FINDLEY (1993) and calculated the percentage of each group occurring in each habitat. Finally, I compared the bat communities of the Accra Plains to those reported in the literature from other areas in Ghana and West and Central Africa. A discussion of new records of bat species from Ghana has been published elsewhere (DECHER et al. 1997).

Results

Numbers caught

A total of 252 bats assignable to 31 species was caught (Tab. 1). Of these, 229 bats (28 species) were caught on the Accra Plains and 23 (7 species) were caught at Yendi and Bimbila in Northern Ghana. Five species were fruit bats (Megachiroptera: Pteropodidae) and the remaining 23 species belonged to seven families of Microchiroptera (Fig. 2). Of all bats captured on the Accra Plains, 31% were caught at the Shai Hills North savanna site adjacent to a water hole. This site also had the highest number of different species (16) of all sites. Bimbila in northern Ghana had the highest capture rate of 3.26 bats per net night and net unit ($NN^{-1}NU^{-1}$), followed closely by Shai Hills North with 3.23 bats $NN^{-1}NU^{-1}$. The lowest capture rate, 0.38 bats $NN^{-1}NU^{-1}$, occurred at Adumanya Sacred Grove. Capture rates inside forests were generally lower than those in open savanna habitats and those near water surfaces. Large numbers (>1 000 individuals) of straw-colored fruit bats (*Eidolon helvum*) were present in the canopy of Adumanya Sacred Grove twice during the study period but the species was not included in the calculations because *E. helvum* could not be sampled with the mist nets set on the forest floor. Colonies of many thousand individuals of *E. helvum* also appeared in the capital city of Accra during part of the study period (1991/92) near the Sankara Circle and the Military Hospital area. Also not included in the diversity calculations were 52 roof-dwelling molossids (*Tadarida*

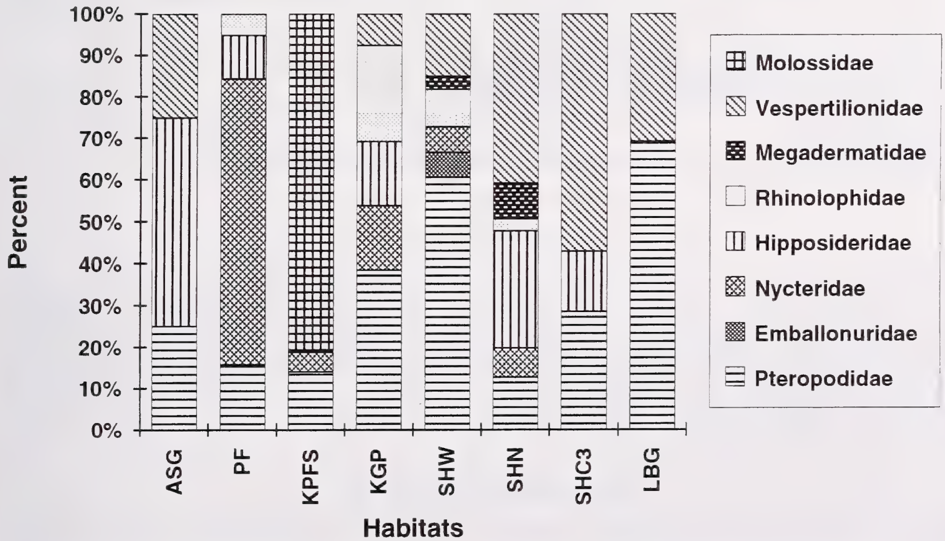


Fig. 2. Distribution of bat families among Accra Plains localities. (See text for abbreviations).

condylura) caught near the Kpong Fire Protection Site as they emerged from underneath the roof of a guest house. The two northern Ghanaian sites included three species that I did not find on the Accra Plains, two molossid bats (*Tadarida nigeriae* and *T. pumila*) and one vespertilionid (*Scotophilus leucogaster*).

Diversity Indices

Diversity was highest in the Shai Hills Resource Reserve where I found 8 species (1-D = 0.61; H′ = 2.04) at the southwestern end (SHW) of the reserve and 16 species (1-D = 0.90; H′ = 3.36) at the northeastern end (SHN, also called "Pillar 14"). Diversity was lowest at Bimbila in Northern Ghana with two species (1-D = 0.32; H′ = 0.72) and at the Legon Botanical Garden where only three species were caught (1-D = 0.46; H′ = 1.14). The number of equally common species (N1) was 10.3 for Shai Hills North and 2.2 for Legon Botanical Garden (Tab. 2). It should be noted here that the diversity indices are highly sensitive to one very abundant species. For example, if an arbitrary estimate of 1 000 individuals of the canopy-roosting *E. helvum* were included at Adumanya Sacred Grove, Simpson's diversity index (1-D) would be reduced from 0.66 to 0.016.

Table 2. Numbers per net night and net unit, diversity, and evenness indices for bats caught at ten localities in Ghana. (See text for abbreviations).

	Locality									
	ASG[a]	PF	KPFS	KGP	SHW	SHN	SHC3	LBG	YEN	BIM
Average No. of Bats $NN^{-1}NU^{-1}$	0.38	0.63	0.76	1.35	1.34	2.69	1.52	2.83	2.76	3.26
S = Total No. of species caught	5	5	5	7	8	16	5	3	6	2
Simpson's Index $D = \Sigma m^2$[b]	0.34	0.34	0.31	0.20	0.39	0.10	0.27	0.54	0.19	0.68
1-D[c]	0.66	0.66	0.69	0.80	0.61	0.90	0.73	0.46	0.81	0.32
Shannon-Wiener Index $H' = -\Sigma (p_i) (\log_2 p_i)$[d]	1.75	1.89	1.83	2.57	2.04	3.36	2.13	1.14	2.50	0.72
$N1 = e^{H'}$[e]	3.4	3.7	3.6	5.9	4.1	10.3	4.4	2.2	5.7	1.6
$H'_{Max} = \log_2 S$	2.32	2.32	2.32	2.81	3.00	4.00	2.32	1.58	2.58	1.00
Eveness $J' = H'/H'_{Max}$	0.75	0.82	0.79	0.91	0.68	0.84	0.92	0.72	0.97	0.72

[a] *Eidolon helvum* excluded from calculations.
[b] Probability of picking two organisms that are the same species.
[c] Probability of picking two organisms that are different species.
[d] Average degree of uncertainty in predicting to what species an individual chosen at random from a sample will belong.
[e] Number of equally common species that would produce the same diversity as H′.

Correlations

Pearson's correlation coefficients for distance to water and distance to nearest escarpment versus species number and diversity indices were not statistically significant ($p > 0.05$; Tab. 3). Only between canopy cover and number of individuals per net night and net unit was there a statistically significant negative correlation at the 0.05 level ($r = -0.77$; $p = 0.041$). Thus, 59% ($r^2 = 0.593$) of the variation in number of individuals $NN^{-1}NU^{-1}$ could be explained by variation in canopy cover.

Foraging-trophic categories

Figure 3 shows how the species at each locality fall into five foraging-trophic categories. The two sacred groves differed greatly from each other in species composition. The dense

Table 3. Pearson's correlation coefficients of distance to water, distance to nearest escarpment, and canopy cover, versus number of species and diversity indices of bats. For definitions see text.

Bat Species Diversity Measures	Habitat Variables		
	Distance to Water	Distance to Escarpment	Percent Canopy Cover
No. of Species S	–0.04	–0.49	–0.56
Simpson's Index 1-D	0.08	–0.43	–0.49
Shannon-Wiener H′	0.07	–0.48	–0.55
Eveness Index	–0.25	0.04	–0.25
Numbers of bats per net night per net unit	–0.57	0.11	–0.77*

* $p < 0.05$

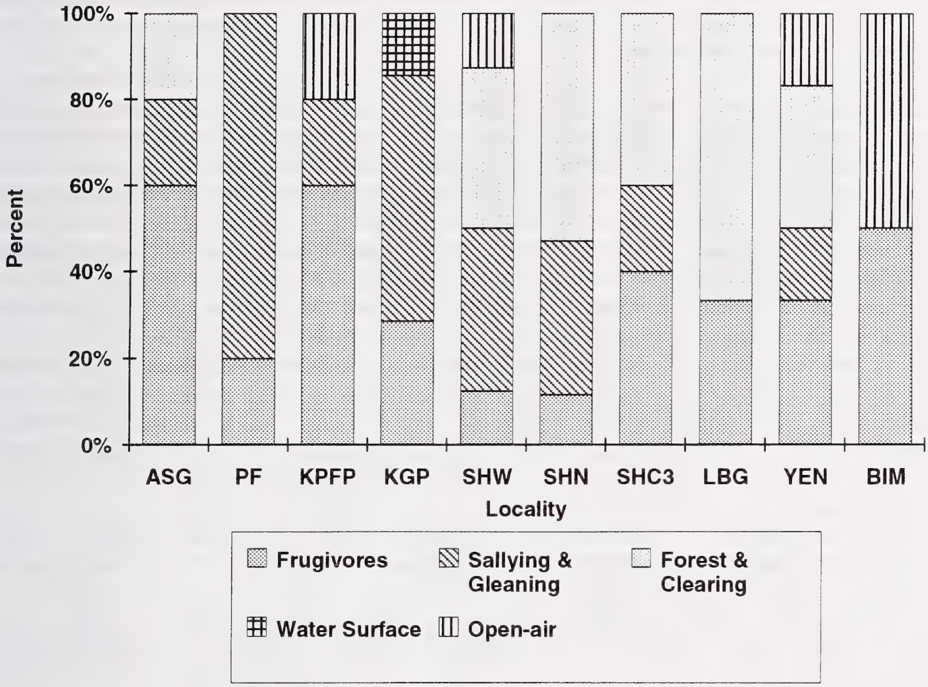


Fig. 3. Foraging-trophic groups of 31 species of bats at 10 localities in Ghana. (See text for abbreviations).

thicket of Pinkwae Forest was characterized by sallying-and-gleaning bats, mainly Nycteridae, and by the absence of the Vespertilionidae. The more open primary forest character of Adumanya Sacred Grove permitted the presence of more frugivores and forest-and-clearing species. Three of the five species present at Adumanya Sacred Grove were frugivores. *Hipposideros cyclops* represents the sallying-and-gleaning insectivores and *Glauconycteris poensis* the forest-and-clearing aerial insectivores. At Pinkwae Forest, frugivores were represented only by *Micropteropus pusillus*, whereas the sallying-and-gleaning insectivores dominated in the dense thicket vegetation and consisted of one hipposiderid, two nycterids, and one rhinolophid.

The two fire-protected sites on the northeastern Accra Plains were also quite different in origin and vegetational history. Inside the relatively recent (1957) Kpong Fire Protection Site the sallying-and-gleaning bats were only represented by *Nycteris macrotis*, and the frugivores only by the ubiqituous *Micropteropus pusillus*, whereas at the forest edge I also caught *Epomops franqueti* and *Myonycteris torquata*. Outside of the forest the open-air aerial insectivore category was represented by *Tadarida condylura*, which had many roosting opportunities in the buildings of the Agricultural Research Station. At the Kpong Gmelina Plantation the sallying-and-gleaning insectivores were represented by the same three families as at Pinkwae Forest. Here, all frugivores were caught just outside the forest. *Myotis bocagei*, a water-surface forager, was caught only at this location, perhaps because of proximity to the Volta River and Kpong Reservoir. Another reason may be that certain plant species that serve as roosting places for *M. bocagei* are more abundant in this northeastern part of the Accra Plains than in the remaining parts that receive less rainfall. Examples of such plants reported in the literature are the young rolled-up leaves of the banana plant (*Musa* sp.; Brosset 1976) and the funnel-shaped leaves of certain Araceae (for example, *Cytrospermum senegalense*; Sanborn 1949; Rosevear 1965).

The more open sites in the Shai Hills Reserve were characterized by high diversity that resulted mainly from the presence of several vespertilionids. Sallying-and-gleaning and forest-and-clearing species share the habitat at all localities with frugivores. The northwestern site at Camp III (SHC3), sampled for one night at the beginning of the field season, was similar to the northeastern Shai Hills site (SHN). The sallying-and-gleaning *Hipposideros commersoni* was caught only at these two sites. This bat has been characterized as a species that "will forage in moderate clutter, but will not be capable of entering thick vegetation" (Aldridge and Rautenbach 1987). This is one of the largest insectivorous bats of Africa, second in size only to *Saccolaimus peli* (Rosevear 1965), which is found in Ghanaian forests but has not yet been collected on the Accra Plains. Near rock faces on the slope I also caught *Taphozous perforatus*, an open-air-aerial insectivore that roosts in caves and rock-crevices. A large colony of this species roosted in a cave formed by huge boulders in the northern Shai Hills. Judging from the guano stain on the ceiling inside some of the park buildings, other open-air-aerial insectivores (e. g. *Tadarida* sp.), must have been present at the Shai Hills Resource Reserve, but they were never caught.

Only the frugivore *Epomophorus gambianus* and two forest-and-clearing vespertilionids, *Scotophilus dinganii* and *Eptesicus guineensis*, were caught at Legon Botanical Garden. Foraging-trophic communities at the northern Ghanaian garden site at Yendi resembled those at Shai Hills West, whereas the Bimbila site was shared by *E. gambianus* and one open-air-aerial insectivore, *Tadarida nigeriae*, a common savanna species.

Reproductive condition

Sixty-eight percent of male and female bats caught on the Accra Plains during the dry season (November to March) were non-breeding and 32% were in breeding condition. At the beginning of the rainy season (April to June) the values were 54.5% and 45.5%, respectively, but the difference was not statistically significant ($X^2 = 2.55$, $p = 0.11$, 1 d. f.). More conservative estimates using only lactation and embryos in female bats preserved as vouchers were 34.1% breeding and 65.9% non-breeding during the dry season versus 60% and 40%, respectively, during the rainy season ($X^2 = 3.67$, $p = 0.055$, 1 d. f.). During November 1991, 90% (18) of the female bats collected in Northern Ghana were non-breeding and 10% (2) were in breeding condition.

Discussion

My observations on the Accra Plains confirmed the presence of five of the 13 species of fruit bats known from Ghana (Tab. 4; Mickleburgh et al. 1992). Most common were the small *Micropteropus pusillus* in more forested habitats and *Epomophorus gambianus* in more open habitats. The seasonal appearance of large colonies of *Eidolon helvum* on the Accra Plains seems to be part of the migration pattern of this species which has been discussed by Thomas (1983) for the Ivory Coast and other areas of Africa. One species not reported by Booth (1959), a male *Myonycteris torquata*, was caught at the beginning of the rainy season near the Kpong Fire Protection Site on 2 June 1992. Other specimens of this species known from the Accra Plains include two males caught at Legon on 30 November and 1 December 1967 (USNM unpubl. records). In his study of the migration of fruit bats, Thomas (1983) observed that during the rainy season predominantly male *M. torquata* migrate from the forest into the savanna. *Epomops franqueti* was characterized as “a rare visitor occurring mainly in the sub-scarp zone” (Booth 1959), but there are several specimens from Legon and Achimota at the USNM that also were reported in a taxonomic work by Bergmans (1989). *Rousettus aegyptiacus* and *Nanonycteris veldkampi* were not encountered during this study. Booth (1959) described *R. aegyptiacus* as limited to “Krobo Hill, where it roosts in caves.” This fruit bat is known from several localities in the forest zone surrounding the Accra Plains (USNM, unpubl. records) and also from Mole National Park (Marshall and McWilliams 1982). *Nanonycteris veldkampi* was observed and collected at Legon from July to September 1967 (USNM, unpubl. records). In his study of the migration of fruit bats in the Ivory Coast, Thomas (1983) observed that this species was “rare or absent” at two savanna sites during the dry season but common in the forest zone. Similarly, this species was the most abundant fruit bat (followed by *Micropteropus pusillus*) during the rainy season at Mole National Park in Northern Ghana, but was found to be absent during the dry season and “to fly higher and thus may be less likely to be netted” (Marshall and McWilliams 1982). Findley (1993) also warned that “In arid regions, samples may be heavily biased in favor of species that visit water sources.”

Table 4. Species of fruit bats (Pteropodidae) occurring in Ghana.

Species	Accra Plains	Mole National Park[c]	Other localities
Eidolon helvum	✔[a, b]	✔	
Epomophorus gambianus	✔[a, b]	✔	
Epomops buettikoferi			✔
Epomops franqueti	✔[a, b]		
Hypsignathus monstrosus			✔
Megaloglossus woermanni			✔
Micropteropus pusillus	✔[a, b]	✔	
Myonycteris torquata	✔[a]	✔	
Nanonycteris veldkampi	✔[b]	✔	
Rousettus angolensis		✔	
Rousettus aegyptiacus	✔[b]	✔	
Scotonycteris ophiodon			✔
Scotonycteris zenkeri			✔

[a] this study
[b] Booth (1959)
[c] Marshall and McWilliams (1982)

Three microchiropteran species were caught only in the sacred groves. *Hipposideros cyclops* was collected previously on the Accra Plains at the Shai Hills and at Krobo Hill (Booth 1959; USNM unpubl. records). *Glauconycteris poensis* was known only from various southern Ghanaian localities outside the Accra Plains, whereas *Hipposideros abae* was recorded previously only from Butre in the Western Region of Ghana (4°49′ N 1°55′ W; USNM No. 414 239, unpubl. record) and from the coastal town of Anomabu (= Anomabo) in the Central Region (Cansdale 1948; Hayman 1945).

The present study represents only a tentative analysis of the composition of bat communities in different habitat types because I was unable to sample bats with mist nets above a height of three meters. The overall number of 28 species from the Accra Plains is comparable to numbers from other studies of geographically restricted localities in Africa. Verschuren (1957) found 38 species of bats in two years at Garamba National Park in northeastern Zaire, a savanna and grassland area about twice the size of the Accra Plains. A study in the thornscrub and riverine vegetation of southern Kenya found strong seasonal differences of faunal composition for 25 species of bats and led the authors to suspect a seasonal migration pattern for many species (O'Shea and Vaughan 1980). Diversity indices in African primary forest is not much higher than in the savanna. For example, Brosset (1966) found 27 species in 11 months in northeastern Gabon, and Jones (1971) found 22 species throughout Rio Muni in central Africa. I compared local (alpha) diversities on the Accra Plains with diversities calculated from published survey results from Benin, Burkina Faso, Ivory Coast, and Togo (Tab. 5; De Vree 1971; Koopman et al. 1978; Robbins 1980). In this comparison Shai Hills North (SHN) on the Accra Plains had the highest diversity with 16 species, a Simpson's Index 1-D of 0.9, and a Shannon-Wiener Index of H′ of 3.36 compared to the highest non-Ghanaian diversity values of 15 species, 0.86, and 3.23, respectively, for Nobere, Burkina Faso (Koopman et al. 1978), and 15 species, 0.86, and 3.13, respectively, for Bimbereke, Benin (Robbins 1980). Although this comparison has to be viewed with caution, because numbers of net nights and net units are not available for the non-Ghanaian sites, it can be concluded that in comparison with other savanna localities in West Africa the Accra Plains host an abundant chiropteran fauna. The reproductive data suggest that the strong seasonal climate of northern Ghana might lead to a more seasonal breeding pattern than on the Accra Plains. In an earlier study at Mole National Park the fruit bats *Micropteropus pusillus*, *Epomophorus gambianus*, and *Nanonycteris veldkampi* gave birth "towards the beginning of the rainy season" (Marshall and McWilliam 1982) but at least one of the microchiropteran species at Mole (*Tadarida pumila*) may be a less seasonal breeder with polyoestrus females having up to five successive pregnancies per year (McWilliam 1987).

Figure 4 demonstrates how the cumulative number of species leveled off during six nights of netting at Shai Hills North between 13 January and 18 May 1992. Only three species were added to the total after the first night of netting and no new species were found after the third night. There is no method for determining the absolute number of bats at a site (Findley 1993). Referring to a note Grinnell (1922) made about bird communities, Findley (1993) contended that we would eventually find every species at every location given enough time and the mobile nature of bats.

My results from the Accra Plains seem to support the hypothesis that local diversity can be highly variable within a relatively small region depending on the structure of the habitat. We can reject the hypothesis that bat communities on the Accra Plains are randoms assemblages. More complex communities seem to be determined by more than one habitat factor. Numbers of species and diversity indices appeared to be negatively correlated with canopy cover. If degree of canopy closure is indicative of dense vegetation, this is contrary to findings at Mole National Park in Northern Ghana where "denser vegetation apparently favoured netting bats" (Marshall and McWilliams 1982). On the Accra Plains, most species seemed to coexist near water holes in patchy habitat of open grass-

Table 5. Local (alpha) diversities of bat communities in central West Africa

Locality	Country	Coordinates	Total No. of bats caught	No. of species	Simpson's Index 1-D	Shannon-Wiener H′	Source
Bimbereke	BENIN	10°14′ N 02°40′ E	113	15	0.86	3.13	Robbins (1980)
Guene	BENIN	11°44′ N 03°13′ E	106	10	0.80	2.63	Robbins (1980)
Segbana	BENIN	10°56′ N 03°42′ E	40	10	0.78	2.60	Robbins (1980)
Djipologo	BURKINA FASO	10°56′ N 3°07′ W	47	8	0.76	2.41	Koopman et al. (1978)
Konankira	BURKINA FASO	12°54′ N 3°53′ W	52	8	0.73	2.27	Koopman et al. (1978)
Nobere	BURKINA FASO	11°26′ N 1°10′ W	73	15	0.86	3.23	Koopman et al. (1978)
Adiopodoumé	COTE D'IVOIRE	05°19′ N 04°01′ W	38	12	0.84	3.04	de Vree (1971)
Kpong	GHANA	6°08′ N 0°04′ E	13	7	0.81	2.57	this study
Shai Hills North	GHANA	5°57′ N 0°04′ E	71	16	0.90	3.36	this study
Yendi	GHANA	9°25′ N 0°04′ W	8	6	0.81	2.50	this study
Ezime	TOGO	07°29′ N 00°56′ E	59	11	0.71	2.38	Robbins (1980)
Pewa	TOGO	09°17′ N 01°14′ E	94	8	0.66	1.58	Robbins (1980)

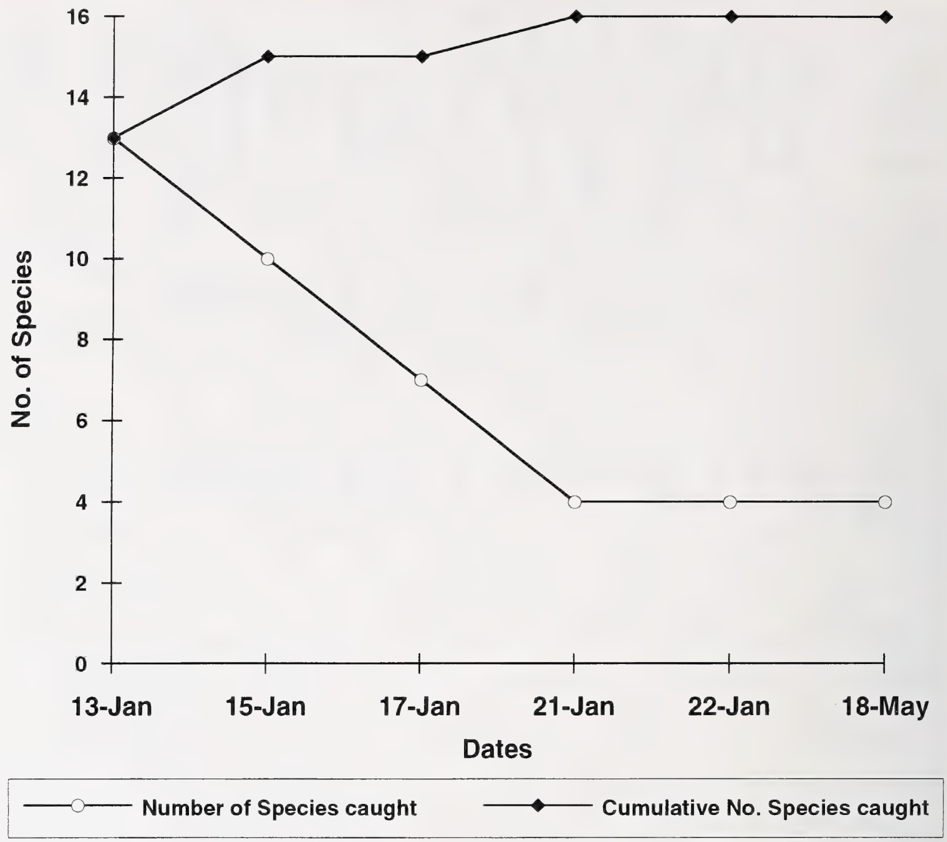


Fig. 4. Cumulative increase of number of bat species at Shai Hills North (SHN; "pillar 14") during six nights of netting.

land, thicket, and dry forest edge. Closed forest, which on the Accra Plains is best preserved in the sacred groves, was less species-rich but seemed to be the preferred habitat for a few species that were not captured elsewhere.

Acknowledgements

Thanks to L. K. Bahian of Mole National Park and D. A. Schlitter, Carnegie Museum of Natural History, for assistance in the field and invaluable discussions and to my advisor, E. C. Birney, at the Bell Museum of Natural History for many helpful comments on the manuscript. I am grateful to G. Punguse, Ghana Department of Game and Wildlife, for permission to work in the Shai Hills Game Production Reserve; to S. Effah of the Yendi District Forestry Station; E. O. Darkwa and J. W. Oteng for permission to work at the Kpong Agricultural Research Station and housing; Chief Nii Laryea Akuete VIII and J. O. Laryea of Katamanso for access to Pinkwae Forest; and chief Nana Opata III of Doryum and Mr. Nathan Narh Nanoo for access to Adumanya Sacred Grove. Special thanks to E. C. Briandt of Mamobi, Accra; to A. and K. Hofmann-Landis of Katamanso; and my wife, Laurel Decher.

Financial support was provided by the Dayton/Wilkie and Sigerfoos Funds of the University of Minnesota, and the M. Graham Netting Research Fund of the Carnegie Museum of Natural History, Pittsburgh.

Zusammenfassung

Fledermausgesellschaften und ihre Verbreitung auf der Accra-Ebene Ghanas, Westafrika

Die Fledermaus-Fauna Ghanas wurde mit Hilfe von Japannetzen an acht verschieden Lokalitäten der Accra-Ebene sowie zwei Lokalitäten in Nord-Ghana untersucht. Insgesamt wurden 252 Fledermäuse gefangen, fünf Arten von Flughunden (Pteropodidae) und 26 Arten aus sieben Familien der Microchiropteren. *Glauconycteris poensis*, *Hipposideros cyclops* und *Hipposideros abae* wurden nur in von traditionellen Tabus geschützten „heiligen Hainen" (sacred groves) gefangen. *Taphozous perforatus* fand sich nur in der Nähe von Felskliffen im staatlich geschützten Shai Hills Wildreservat, während *Myonycteris torquata* und *Myotis bocagei* nur am Rande einer *Gmelina*-Monokultur im Nordostteil der Accra Ebene, am Unterlauf des Volta Flusses, vorkamen. Obwohl Korrelationen zwischen Biotopeigenschaften und Artenzahl und Diversität nicht statistisch signifikant waren, schien verhältnismäßig offene Savanne und Wassernähe die Diversität und Abundanz der Fledermäuse zu begünstigen. Artenzahl und Diversitätsindices waren geringfügig höher als in anderen Savannenregionen Westafrikas. Es wird dringend empfohlen den anhaltenden Schutz der „heiligen Haine" auf lokaler Ebene, möglichst mit Hilfe eines landesweiten Schutzprogrammes zu unterstützen.

References

Aldrige, H. D. J. N.; Rautenbach, I. L. (1987): Morphology, echolocation and resource partitioning in insectivorous bats. J. Anim. Ecol. **56**, 763–778.

Ayensu, E. S. (1974): Plant and bat interaction in West Africa. Annals Missouri Bot. Gard. **61**, 702–727.

Baker, H. G.; Harris, B. J. (1957): The pollination of Parkia by bats and its attendant evolutionary problems. Evolution **11**, 449–460.

Baker, H. G.; Harris, B. J. (1959): Bat pollination of the silk cotton tree, *Ceiba pentandra* (L.) Gaertn, (sensu lato), in Ghana. J. West Afr. Sci. Assoc. **5**, 1–9.

Bergmans, W. (1989): Taxonomy and biogeography of African fruit bats (Mammalia, Megachiroptera). 2. The genera *Micropterus* Matschie, 1899, *Epomops* Gray, 1870, *Hypsignathus* H. Allen, 1861, *Nanonycteris* Matschie, 1899, and *Plerotes* Andersen, 1910. Beaufortia **39**, 89–153.

Booth, A. H. (1959): On the mammalian fauna of the Accra plain. J. West. Afr. Sci. Assoc. **5**, 26–36.

Brosset, A. (1966): Les chiroptères du Haut-Ivindo (Gabon). Biol. Gabonica **1**, 47–86.

Brosset, A. (1976): Social organization in the African bat, *Myotis bocagii*. Z. Tierpsychol. **42**, 50–56.

Cansdale, G. S. (1948): Provisional checklist of Gold Coast mammals. Accra: Government Printing Dept.

Carson, W. P.; Abbiw, D. K. (1990): The vegetation of a fire protection site on the northern Accra Plains, Ghana. Afr. J. Ecology **28**, 143–146.

Decher, J. (1996). Small mammal communities and their conservation on the Accra Plains of Ghana. Ph. D. dissert., Univ. Minnesota, St. Paul, Minnesota.

Decher, J.; Schlitter, D. A.; Hutterer, R. (1997): Noteworthy records of small mammals from Ghana with special emphasis on the Accra Plains. Annals of Carnegie Museum (in press).

De Vree, F. (1971): Notes sur une collection de Chiroptères ouest africaines, principalement de la Côte D'Ivoire. Rev. Zool. Bot. Afr. **83**, 31–49.

Fenton, M. B.; Boyle, N. G. H.; Harrison, T. M.; Oxley, D. J. (1977): Activity patterns, habitat use, and prey selection by some African insectivorous bats. Biotropica **9**, 73–85.

Finley, J. S. (1993): Bats: a community perspective. Cambridge: Cambridge Univ. Press.

Findley, J. S.; Black, H. L. (1983): Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology **64**, 625–630.

Grinnell, J. (1922): The role of the accidental. Auk **39**, 373–380.

Harris, B. J., Baker, H. G. (1958): Pollination of *Kigelia africana* Benth. J. West Afr. Sci. Assoc. **4**, 25–30.

Harris, B. J.; Baker, H. G. (1959): Pollination of flowers by bats in Ghana. Niger. Field **14**, 151–159.

Hayman, R. W. (1945): A new *Scotonycteris*, with notes on other Gold Coast bats. Annals and Magazine of Natural History, Ser. 11, **7**, 766–775.

Jones, C. (1971): The bats of Rio Muni. J. Mammalogy **52**, 121–140.

Koopman, K. F.; Mumford, R. E.; Heisterberg, J. F. (1978): Bat records from Upper Volta, West Africa. Amer. Mus. Novitates **2643**, 1–6.

Krebs, C. J. (1989): Ecological Methodology. New York: Harper Collins Publ.
Lack, A. (1978): The ecology of the flower of the savanna tree *Maranthes polyandra* and their visitors, with particular references to bats. J. Ecol. **66**, 287–295.
Lieberman, D. (1979): Dynamics of forest and thicket vegetation on the Accra Plains, Ghana. Diss. thesis, Univ. Ghana, Legon.
Marshall, A. G.; McWiliams, A. N. (1982): Ecological observations on epomophorine fruit-bats (Megachiroptera) in West African savanna woodland. J. Zool. (London) **198**, 53–67.
McWilliams, A. N. (1987): Polyoestry and postpartum oestrus in *Tadarida* (*Chaerophon*) *pumila* (Chiroptera: Molossidae) in northern Ghana, West Africa. J. Zool. (London) **213**, 735–739.
McWilliams, A. N. (1988): Social organisation of the bat *Tadarida* (*Chaerophon*) *pumila* (Chiroptera: Molossidae) in Ghana, West Africa. Ethology **77**, 115–124.
McWilliams, A. N. (1989): Emergence behavior of the bat *Tadarida* (*Chaerophon*) *pumila* (Chiroptera: Molossidae) in Ghana, West Africa. J. Zool. (London) **219**, 698–701.
Mickleburgh, S. P.; Hutson, A. M.; Racey, P. A. (1992): Old World fruit bats: an action plan for their conservation. Gland, Switzerland: IUCN.
O'Shea, T. J.; Vaughan, T. A. (1980): Ecological observations on an East African bat community. Mammalia **44**, 485–496.
Robbins, C. B. (1980): Small mammals of Togo and Benin. I. Chiroptera. Mammalia **44**, 83–88.
Rosevear, D. R. (1965): The bats of West Africa. London: The British Museum (Natural History).
Sanborn, C. C. (1949): Extension of range of the African bat, *Myotis bocagei cupreolus* Thomas. J. Mammalogy **30**, 315.
Sas Institute, I. (1982): SAS user guide: statistics. 1982 ed. Cary, North Carolina: SAS Institute, Inc.
Schmitt, K.; Adu-Nsiah, M. (1993): The vegetation of Shai Hills Resource Reserve (Forest Resource Management Project 9786): Ghana Wildlife Department/IUCN Accra Ghana.
Swaine, M. D.; Hawthorne, W. D.; Orgie, T. K. (1992): The effects of fire exclusion on savanna vegetation at Kpong, Ghana. Biotropica **24**, 166–172.
Thomas, D. W. (1982): The ecology of an African savanna fruit bat community: resource partitioning and role in seed dispersal. Ph. D. dissertation, Univ. Aberdeen, UK.
Thomas, D. W. (1983): The annual migrations of three species of West African fruit bats (Chiroptera: Pteropodidae). Can. J. Zool. **61**, 2266–2272.
Verschuren, J. (1957): Écologie, biologie et systématique des cheiroptères. Expl. Parc Nat. Garamba. Mission H. de Saeger et al. 1949–1952, **7,** 1–473.
Whittaker, R. H. (1972): Evolution and measurement of species diversity. Taxon **21**, 213–251.
Willig, M. R.; Mares, M. A. (1989): A comparison of bat assemblages from phytogeographic zones of Venezuela. In: Patterns in the structure of mammalian communities. Ed. by. D. W. Morris, Z. Abramsky, B. J. Fox, and M. R. Willig. Spec. Publ., The Museum, Texas Tech Univ. **28**, 59–67.

Author's address: Jan Decher, Ph. D., Bell Museum of Natural History, University of Minnesota, 100 Ecology, St. Paul, Minnesota 55108, USA

Z. Säugetierkunde **62** (1997) 143–151

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Population structure of the otter, *Lutra lutra*. Parameters and model for a Central European region

H. ANSORGE, R. SCHIPKE, and O. ZINKE

Staatliches Museum für Naturkunde, Görlitz and Museum der Westlausitz, Kamenz, Germany

Receipt of Ms. 26. 07. 1996
Acceptance of Ms. 01. 11. 1996

Abstract

A sample of 225 dead otters – mostly road-kills – was collected from 1980 to 1995 in Upper Lusatia („Oberlausitz", Germany). All otter carcasses were examined for signs of reproduction and were aged according to incremental cementum lines. The data obtained were combined with field observations of cubs to endeavour the modelling of real population parameters.

In the Upper Lusatia region the mean litter size of the otter (2.7) and the proportion of early losses of cubs (24%) appeared to be at a normal level compared to different data from the European area. The proportion of adult non-breeding females amounted to 40%. Among otter carcasses the males predominated especially in younger age classes. In Upper Lusatia, otters live to a very old age, up to 16 years, and the sample shows a high fraction of older animals.

By using the obtained parameters a population model for the otter in the Upper Lusatia region was developed. The age pyramid of this model is relatively stretched with a female-biased sex ratio among the adults, thus compensating for the low proportion of breeding females.

Mortality is very high during the first year, but very few otters die in middle ages of life. Except for juveniles the survivalship curve shows a convex trend typical for long-lived large mammals.

Introduction

The Eurasian otter, *Lutra lutra* (LINNÉ, 1758), belongs to the most endangered mammalian species of Europe. In western and central parts of its European area of distribution the population splittings have been followed by considerable decrease or extinction (REUTHER 1992). Therefore, many investigations were directed to the problems of conservation biology of this species in the last twenty years. Nevertheless, there is still little knowledge on the population ecology of the otter.

Very useful data, analyses, and conclusions were published by HEGGBERGET (1988), KRUUK and CONROY (1991), HEGGBERGET and CHRISTENSEN (1994) and ROSOUX and TOURNEBIZE (1995) based on samples of otter carcasses. In addition, SIDOROVICH (1991) gave interesting results using direct observations to assess the population structure and dynamics of the otter in Byelorussia.

However, most of these studies concerning population ecology of the otter were carried out in northern and eastern European regions. There is still a lack of information on the structure, natality, and mortality of Central European populations living in destroyed habitats and fragmented areas. Only the analyses of the material collected by the Zoological Institute of Halle have resulted in initial insight into the population structure of the otter in eastern Germany (Stubbe 1989; Uthleb et al. 1992). However they are also based on otter carcasses and reflect only the sample of dead otters discovered.

The aim of the present study in the Upper Lusatia region was to establish the modelling of population parameters by combining sample data and records from field observations. This model should adequately mirror the living population to support the species conservation program for the otter in Saxony.

Material and methods

Sample and observation area

The „Oberlausitz" region – Upper Lusatia – in Saxony (Germany) is inhabited by one of the most numerous otter populations; further west otters do not occur. The area of about 5 000 km^2 in the southeast of eastern Germany encompasses different landscapes ranging from a lowland plain rich in ponds and forests to hilly countryside and wooded highlands. There is a centre of otter reproduction in the „Upper Lusatian Pond District" where a multitude of fish farms guarantee excellent feeding conditions for the otter. Surrounded mostly by reeds, old trees, and bushes these carp ponds are connected by extensive ditches with natural bank structures. In the other landscapes of Upper Lusatia without large numbers of fish ponds, the otter lives at lower density suggesting regular migration from the Pond District (Ansorge 1994).

Sample material

A total of 225 otter carcasses was collected from 1980 to 1995. Most of them were found in the Pond District. The main cause of death was road traffic (64% of the discovered otters) having increased up to 85% in the last few years. Otters were delivered at all times of the year with a distinct peak in autumn caused by draining of the ponds.

Reproduction and age analysis

Otter carcasses were dissected and sex was determined by inspection of internal reproductive organs. Data on female reproduction were obtained by counting numbers of follicles, embryos, placental scars and luteal corpora (Heggberget and Christensen 1994). Date of birth of cubs was determined by estimating developmental stages of embryos and registration of fresh placental scars.

More than 40 observations by a few skilled otter watchers were used to determine the number of cubs accompanying the female.

Litter size as estimated by counting embryos and placental scars was compared to the litter size as obtained by counting living cubs per female using a G-test (Weber 1980).

To separate young and adult otters, age estimation was based on the general obliteration of sutures, the development of the postorbital constriction, the sagittal crest, the bone deposition around canine alveoles and the surface structure of the brain-pun as well as the baculum development and the formation of femur epiphysis (van Bree et al. 1966; Stubbe 1969; Heggberget 1984; Skaren 1987; Uthleb et al. 1992).

The adult otters (i. e. older than 2 years) were aged by the configuration of incremental cementum lines of the upper canine or adjacent teeth. Longitudinal sections by an efficient method of low speed cutting (Driscoll et al. 1985; Ansorge 1995) produce the number of annual lines which are then used to establish definite age classes (Heggberget 1984).

Results and discussion

Sample structure

The sex-age composition of the sample material illustrated in figure 1 shows a relatively stretched age pyramid. Only 28% of the animals died during first year of life. Most animals of the population sample (58%) were adults between 3 and 10 years of age and only few otters (3.1%) reached an age of between 10 and 16 years. The mean age class of all otters found dead was 4.2.

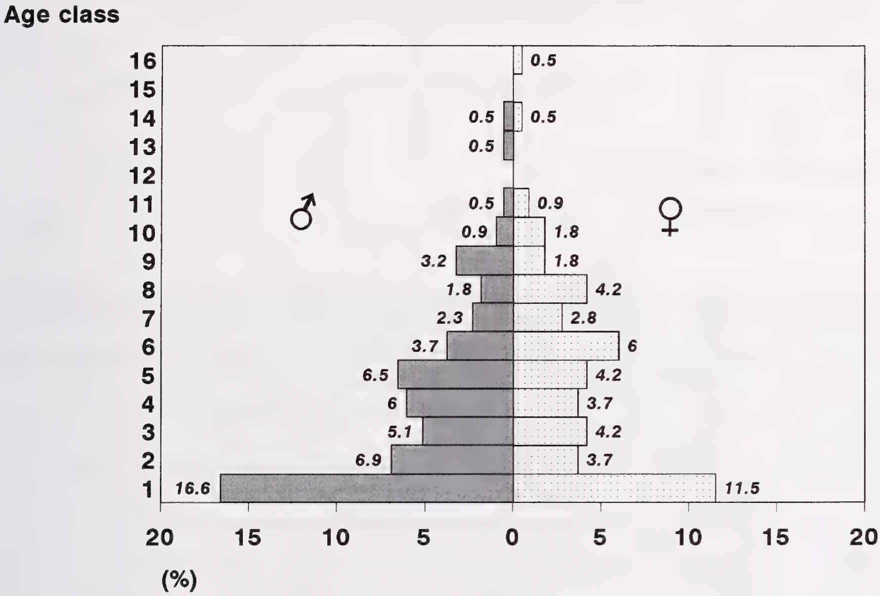


Fig. 1. Sex and age structure of the otter sample (n = 117, percentage of each age class in italics).

The sex ratio of the whole sample amounted to 56% males and 44% females (1.2:1). Especially in age classes 1–5 the males predominated with 60% (1.5:1). In animals older than 5 years there was a clear female-biased sex ratio with only 42% males (0.7:1). However, there was an equal balance of 1.02 males to 1 female amongst all adult otters including animals older than two years.

Reproductive performance

Our observations indicate that females have one litter per year and otter cubs are born throughout the year. In the total sample of 99 female otters (including 61 adults) only 14 specimens between 5 and 10 years old showed countable reproduction signs (Tab. 1). Litter size ranged from 1 to 4 with an average of 2.7 counted by both embryos and placental scars (Tab. 2).

On three occasions, different stages of luteal corpora could be verified (3, 2, 2 corpora lutea). However, with the latter result, there appears to be little use in estimating prenatal mortality. The significant difference ($G = 27.6$, $df = 1$, $p < 0.01$) between the mean litter size counted by embryos or placental scars and the number of living cubs indicates losses of about 24% during the first two months after birth.

Table 1. Age of otter females with reproduction signs from the Upper Lusatia region

age class	5	6	7	8	9	10
total number of females	8	12	6	8	4	4
females with reproduction signs number	1	2	1	5	3	2
%	13	17	17	63	75	50

Table 2. Otter reproduction data of the Upper Lusatia region

number of litters	litter size					
	1	2	3	4	∅	n
counted by embryos	–	2	1	1	2.8	4
counted by placental scars	1	3	4	2	2.7	10
cubs observed	12	20	15	1	2.1	48

From their research on Shetland otters, Kruuk et al. (1991) ascertained a strong correlation between numbers of cubs observed and available prey abundance. This could hint at the social regulation of population density reported from other medium-sized carnivores (e. g. Tullar et al. 1976; Harris 1981). However, Sidorovich (1991) noticed significantly higher fecundity in harvested otter populations of Byelorussia than in protected areas. Compared with the few studies on litter size of otters based on counts of embryos and placental scars, the reproductive parameters from the Upper Lusatia region range at the top of known variation (see Sidorovich 1991; Heggberget and Christensen 1994). The number of 2.7 cubs per litter was only reached in Byelorussia (Sidorovich 1991).

In contrast, the mean number of cubs following a female in Upper Lusatia was 2.1 per litter. This is considerably lower than in other field studies carried out in inland areas (Reuther 1980; Barus and Zejda 1981; Wlodek et al. 1989; Sidorovich 1991). However, Uthleb et al. (1992) reported similarly low mean numbers for otters from all over eastern Germany. Otters of northern coastal areas, such as Norway and the Shetlands, breed even smaller litters (Heggberget and Christensen 1994; Kruuk et al. 1991). The latter authors suggest that food shortage is the main cause of the low reproduction success.

The situation in the Upper Lusatia is more difficult to explain. The high numbers of embryos and placental scars correspond to the very good feeding conditions at most times for the otter foraging mainly in the carp ponds. The high mortality of about 24% of cubs during the first months could be caused by disturbances due to diverse human activities.

In the present study the percentage of non-breeding adult females is calculated by the proportion of gravid females in the total sample of adult females (4/61 see Table 2). However, the proportion of non-breeding adult females was calculated by taking into account that otter embryos are visible only during about 40 days prior to birth (see Stubbe 1993). Thus, the chance of detecting embryos in a gravid female in a given year is 40/365. Consequently, the proportion of gravid vixens is higher than the actually observed percentage, namely 60%.

This low pregnancy rate could be affected by different causes such as PCB contamination (Weber et al. 1991) or density control by reduced fecundity. However, no data concerning these questions are available. In the centre of the Upper Lusatian Pond District otters live in a relatively high density of 1.0–1.3 adults per 10 km^2 (Ansorge 1994). Unfortunately, no other data on the proportion of breeding females are available from compar-

able habitats. Only SIDOROVICH (1991) reported percentages from 27% to 75% of non-breeding females due to over-hunting and very low otter density in Byelorussia.

However, the average number of 1.3 cubs older than two months per adult female seems to be relatively low in the Upper Lusatia. The reason could be the high local otter density and high cub mortality. Basically the higher number of older females results in the considerably high reproduction rate of the whole population.

Construction of the population model

Our model is based on the data of reproduction and the age and sex structure of the otter carcasses. Using these basic data the following assumptions could be made for the construction of the model.

1. A stable otter population without emigrating and immigrating animals is required.
2. All data obtained since 1980 are considered as having been determined at the same time.
3. The probability for adult otters to die by road-kill does not change across age classes (see KRUUK and CONROY 1991).
4. The sex ratio of new born cubs is nearly balanced (HEGGBERGET 1988; SIDOROVICH 1991).

There is however, a critical point in these basic postulates for the population model. The model accepts a stable population without any emigration or immigration. As an unknown part of especially subadults in their second year of life probably leave the increasing population searching for new home ranges. In this case, the real mortality is likely to be lower than estimated. Unfortunately, almost nothing is known about the migration of otters in the Upper Lusatia region.

In the Upper Lusatia region 24% of the cubs die during the first weeks of life probably in balanced sex ratio. The sex-specific mortalities of older juveniles and adults should be represented by the discovered dead otters. However, the greater number of males dying in lower age classes causes a higher percentage of older females in the living population (83.5% females in age class 3–16). This knowledge and the information about the annual percentage of breeding females (60%) and the mean litter size at birth (2.7) permit to estimate the number of newborn cubs per year. The juveniles in age class 1 at the beginning of the first year of life amount to 51.4% of the total population. The portion of the older age classes was directly determined by their percentage in the sample collected since 1980. The age structure given in figure 1 shows some deviations from the general expectation of decreasing otter numbers with increasing age. Therefore, these irregularities were offset by using a curvilinear regression after SOKAL and ROHLF (1995) excluding the juvenile population part (Fig. 2). The sex ratio of a specific age class was determined by deducting the sex-specific losses of the previous age class from its stock. Age class 1 is assumed to start with an equal sex ratio (HEGGBERGET 1988; SIDOROVICH 1991). For calculating the sexes of age class 2 only the dead otters which had been discovered could be used. For earlier losses, an equal sex ratio had to also be assumed.

Population structure

The complete sex and age structure of the population model formed by these deductions is presented in figure 2. It shows a striking bias in favour of the females older than one year. The sex ratio of the reproductive population amounts to 1:3.5 males:females. Despite the high number of non-breeding females, this high percentage of females yields the reproduction rate of somewhat more than 100% for the whole population.

Most investigations on mustelid populations usually show sex ratios biased towards males (see BUSKIRK and LINDSTEDT 1989). Sexual dimorphism in home range size and sex-

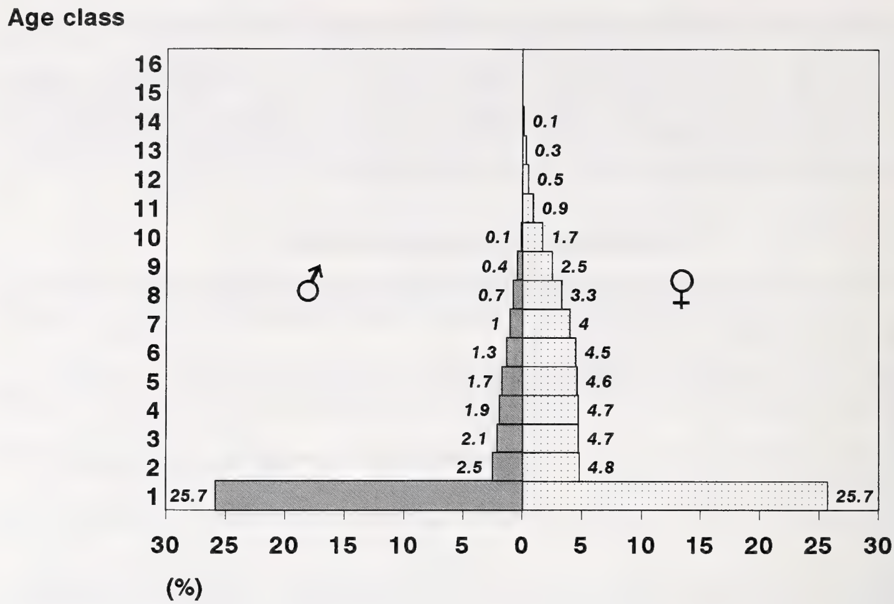


Fig. 2. Model of the population structure (percentage of each age class in italics).

specific behaviour result in a greater presence of male otters in the collected otter carcasses (e. g. Uthleb et al. 1992; Rosoux and Tournebize 1995). Hence, the number of females in the population might predominate over the number of males as demonstrated in a field survey of harvested populations by Sidorovich (1991).

In Upper Lusatia the phenomenon of exploitation has been replaced by road traffic, and local field observations point to the female-biased sex ratio of the model. One good reason for this bias is also given by the switch of the sex ratio in older age classes, because there is a lack of older males in the population and females predominate in the collected sample.

The life expectancy table for the otter in Upper Lusatia is presented in table 3 with pooling the sexes in respective age classes. This table illustrates a very high mortality of about 86% during the first year. This period seems to be the most critical stage in the life cycle of the studied otter population because the mortalities of the following middle age classes remain clearly lower. The juvenile mortality is much higher than in all the other studies, which determined mortality rates only from otters found dead (Sidorovich 1991; Kruuk et al. 1991; Heggberget 1984). Compared with this researche, the present population model from Upper Lusatia starts at birth including the high percentage of early cub losses. Additionally, it should be assumed that cubs are more affected by non-violent death and the chance of these dead cubs to be found is definitely much lower than that of adult carcasses.

Disregarding the juvenile age class, the life expectancy table (Tab. 3) shows a very remarkable trend of survivalship. The respective survivalship curve in figure 3 demonstrates the high initial mortality affecting the juveniles. However, physiological longevity is reached by many otters in Upper Lusatia and the shape of the curve for otters two years old or over shows a slightly convex trend. This means that once otters have survived the first year of life they will probably live to middle or older age. This trend is typical indeed for moderately exploited populations of long-living large mammals (Odum 1971).

Table 3. Life expectancy table (according to ODUM 1971) for the otter in the Upper Lusatia region.

Age class (x)	Number (l_x)	Number dying (d_x)	Mortality rate (q_x)	Life expectancy (e_x)
1	1 000	858	858	1.4
2	142	10	70	6.1
3	132	4	30	5.5
4	128	5	39	4.7
5	123	10	81	3.9
6	113	16	142	3.2
7	97	19	196	2.6
8	78	22	282	2.1
9	56	21	375	1.8
10	35	17	486	1.5
11	18	8	444	1.5
12	10	4	400	1.3
13	6	4	666	0.8
14	2	2	1 000	0.5

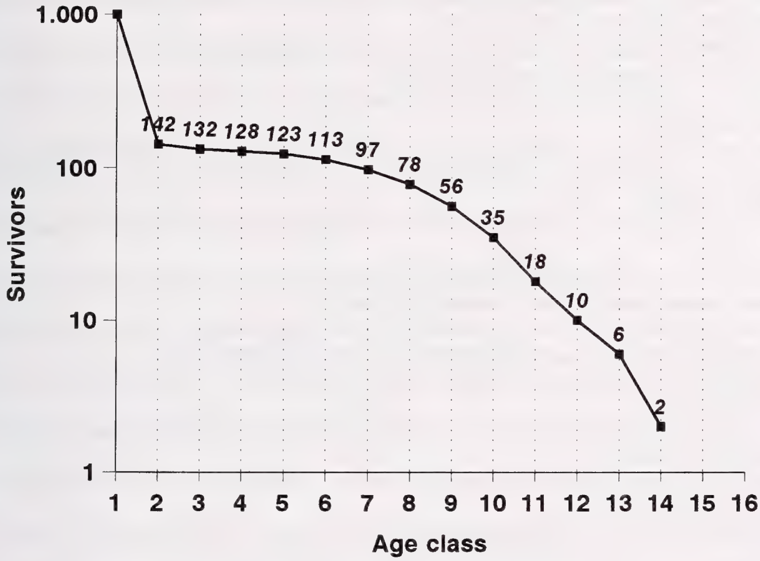


Fig. 3. Survivalship curve of the otter in the Upper Lusatia region.

Acknowledgements

We are very grateful to all the collaborators who are too numerous to be listed here. Our special thanks go to Dr. F. SUCHENTRUNK (Vienna) for the constructive discussion and criticism of former versions of the manuscript and to Prof. Dr. P. J. H. VAN BREE (Amsterdam) for helpful comments and providing special literature. We would like to thank Mr. M. SITTER (Ostritz) for kindly checking and correcting the translation.

Zusammenfassung

Die Populationsstruktur des Fischotters Lutra lutra – Kenngrößen und Modell aus Mitteleuropa

Die Untersuchung beruht auf 225 toten Fischottern, die seit 1980 in der Oberlausitz meist als Verkehrsopfer aufgefunden wurden. Von allen Weibchen wurden die Anzahl vorhandener Embryonen, Uterus-

narben und Gelbkörper registriert. Das Lebensalter der Otter wurde mit Längsschnitten des Zahnzements festgestellt. Durch verläßliche Beobachtungen wurde die Wurfgröße nach lebenden Jungtieren im Freiland ermittelt.

In der Oberlausitz liegen die mittlere Wurfgröße (2,7 nach Embryonen und Uterusnarben) und die postnatalen Verluste (24%) auf dem bisher bekannten Niveau. Der Anteil der nicht reproduzierenden erwachsenen Fähen beträgt 40%.

Bei den Totfunden überwiegen die Männchen besonders in den jüngeren Altersklassen. Die Fischotter erreichen in der Oberlausitz ein recht hohes Alter. Der Anteil älterer Tiere ist unter den Todfunden recht erheblich.

Aus den ermittelten Daten wird ein Populationsmodell für die Fischotter der Oberlausitz entwikkelt. Die Alterspyramide dieses Modells ist recht gestreckt mit starkem Übergewicht der Weibchen in den adulten Altersklassen.

Die Mortalität ist nur im ersten Lebensjahr sehr hoch. Wenige Otter sterben im mittleren Lebensabschnitt. Die Überlebenskurve erwachsener Otter zeigt den convexen Verlauf langlebiger Großsäuger.

References

Ansorge, H. (1994): Zur Situation des eurasischen Fischotters *Lutra lutra* Linné, 1758 im Raum Oberlausitz-Sachsen. Säugetierkdl. Inf. **3**, 617–622.

Ansorge, H. (1995): Notizen zur Altersbestimmung nach Wachstumslinien am Säugetierschädel. Methoden feldökol. Säugetierforschung **1,** 95–102.

Barus, V.; Zejda, J. (1981): The European otter (*Lutra lutra*) in the Czech Socialist Republic. Acta Sc. Nat. Brno **15**, 12, 1–41.

Bree, P. J. H. van; Jensen, B.; Kleijn, L. J. K. (1966): Skull dimensions and the length/weight relation of the baculum as age indications in the common otter *Lutra lutra* (Linnaeus, 1758). Danish Rev. Game Biol. **4**, 97–104.

Buskirk, S. W.; Lindstedt, S. L. (1989): Sex biases in trapped samples of Mustelidae. J. Mammalogy **70**, 88–97.

Driscoll, K. M.; Jones, G. S.; Nichy, F. (1985): An efficient method by which to determine age of carnivores, using dentine rings. J. Zool. (London) **205**, 309–313.

Harris, S. (1981): An estimation of the number of Foxes (*Vulpes vulpes*) in the City of Bristol, and some possible factors affecting their distribution. J. appl. Ecol. **18**, 455–465.

Heggberget, T. M. (1984): Age determination in the European otter *Lutra lutra lutra.* Z. Säugetierkunde **49**, 299–305.

Heggberget, T. M. (1988): Reproduction in the female European otter in central and northern Norway. J. Mammalogy **69**, 164–167.

Heggberget, T. M.; Christensen, H. (1994): Reproductive timing in Eurasian otters on the coast of Norway. Ecography **17**, 339–348.

Kruuk, H.; Conroy, H. J. W. (1991): Mortality of the otters (*Lutra lutra*) in Shetland. J. Appl. Ecology **28**, 83–94.

Kruuk, H.; Conroy, J. W. H.; Moorhouse, A. (1991): Recruitment to a population of otters (*Lutra lutra*) in Shetland, in relation to fish abundance. J. Appl. Ecol. **28**, 95–101.

Odum, E. P. (1971): Fundamentals of ecology. 3. ed. Philadelphia: W. B. Saunders Company.

Reuther, C. (1980): Der Fischotter, *Lutra lutra* L. in Niedersachsen. Naturschutz und Landschaftspflege in Niedersachsen **11**, 1–182.

Reuther, C. (1992): Otter 2000. Eine Vision für den Otterschutz in Deutschland. In: Otterschutz in Deutschland. Ed. by C. Reuther. Habitat (Hankensbüttel) **7**, 113–126.

Rosoux, R.; Tournebize, T. (1995): Analyse des causes de mortalité chez la loutre d'Europe (*Lutra lutra*) dans le Centre-Quest atlantique (France). Cahiers d'Ethologie **15**, 337–350.

Sidorovich, V. E. (1991): Structure, reproductive status and dynamics of the otter population in Byelorussia. Acta theriol. **36**, 153–161.

Skarén, U. (1987): Skull structure in different age groups of otters (*Lutra lutra*) in Central Finland. Kumulus **9**, 42–47.

Sokal, R. R.; Rohlf, F. J. (1995): Biometry. The principles and practice of statistics in biological research. 3. ed. New York: W. H. Freeman and Co.

Stubbe, M. (1969): Zur Biologie und zum Schutz des Fischotters *Lutra lutra* (L.). Arch. Naturschutz Landschaftsforsch. **9**, 315–324.
Stubbe, M. (1989): Verbreitung und Ökologie des Fischotters *Lutra lutra* (L., 1758) in der DDR. Wiss. Beitr. Univ. Halle **1989**, 13–33.
Stubbe, M. (1993): *Mustela vison* Schreber, 1777 – Mink, Amerikanischer Nerz. In: Handbuch der Säugetiere Europas, Bd. 5/2. Ed. by J. Niethammer, J. and F. Krapp. Wiesbaden: Aula-Verlag. Pp. 654–698.
Tullar, B. F.; Berchielli, L. T.; Saggese, E. P. (1976): Some implications of communal denning and pup adoption among red foxes in New York. New York Fish and Wildlife J. **23**, 92–95.
Uthleb, H.; Stubbe, M.; Heidecke, D.; Ansorge, H. (1992): Zur Populationsstruktur des Fischotters *Lutra lutra* (L. 1758) im östlichen Deutschland. Wiss. Beitr. Univ. Halle **1992**, 393–400.
Weber, D.; Weber, J. M.; Müller, H.-U. (1991): Fischotter (*Lutra lutra* L.) im Schwarzwasser-Sense-Gebiet: Dokumentation eines gescheiterten Wiedereinbürgerungsversuchs. Mitt. Naturforsch. Ges. Bern NF **48**, 141–152.
Weber, E. (1980): Grundriß der biologischen Statistik. 8. Aufl., Jena: Gustav Fischer Verlag.
Wlodek, K.; Lapinski, W.; Gielo, M.; Sobolewski, H.; Rösler, A. (1989): Expansion des Fischotters *Lutra lutra* (L., 1758) in Polen. Wiss. Beitr. Univ. Halle **1989**, 44–54.

Authors addresses: Dr. Hermann Ansorge, Staatliches Museum für Naturkunde Görlitz, PF 300 154, D-02806 Görlitz; Reinhard Schipke, Teichweg 4, D-02999 Wartha, and Olaf Zinke, Museum der Westlausitz Kamenz, Pulsnitzer Str. 16, D-01917 Kamenz

Z. Säugetierkunde **62** (1997) 152–157

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The diet of *Microtus pyrenaicus* (De Sélys-Longchamps, 1847) in the western Pyrenees

By E. Castién and J. Gosálbez

Servicio de Conservación de la Naturaleza, Gobierno de Navarra, Pamplona and Departament de Biologia Animal, Universitat de Barcelona, Barcelona, Spain.

Receipt of Ms. 10. 04. 1996
Acceptance of Ms. 19. 12. 1996

Abstract

The diet of *Microtus pyrenaicus* was studied based on the analysis of remains found in 74 stomachs. The most representative type of food in the diet was made up of the aerial vegetative parts of dicotyledons (%N = 59.3). The aerial vegetative parts of monocotyledons also constituted a large part of the diet (%N = 30.0). The remaining food types consisting of flowers, bryophytes, fungi, and seeds of herbaceous plants, contributed 10.7% of the diet (%N). Although the diet was more varied in summer and autumn, the green parts of plants were the greatest source of food throughout the year. Taking into account the surface area occupied by dicotyledon and monocotyledon plants in the meadows, the species makes a positive selection of dicotyledons, favoring these over the monocotyledons. The low values for cumulative diversity and equitability indicate that the species has a stenophagous diet.

Introduction

Microtus pyrenaicus inhabits areas of the Pyrenee Mountains (North Iberian Peninsula). At present little research has been performed on the biology of this species. The data published to date refer to its reproductive cycle (Castién and Gosalbez 1995) and to the characteristics of its habitat (Krapp 1982; Saint-Girons et al. 1978; Gosalbez et al. 1985; Borghi et al. 1994). This is the first study that has been performed the diet of this species.

Material and methods

The study area is located in the Quinto Real Massif (western Pyrenees). The dominant vegetation in this area is an acidophilic *Fagus sylvatica* forest which is in association with *Saxifrago hirsutae-Fagetum sylvaticae* (Braun-Blanquet 1967). Samples were caught mostly in small natural meadows located amid the forest at altitudes ranging between 650 m and 750 m. The average annual precipitation is about 2,138 mm, with the highest levels in spring and autumn. The mean temperature is 8.8 °C. The highest average temperature is in August (16.6 °C) and the lowest in January (2.9 °C).

The vegetative cover of the meadows was estimated by randomly throwing a needle into the grass and recording the species that it hit on each throw (Greigh-Smith 1964).

There are several methods to estimate the proportion of diet components (Obrtel and Holisova 1976; Butet 1985). A critical review of some of these can be found in Hansson (1970). The method used here to prepare the stomach samples was that of Ventura et al. (1989). Each stomach content was sub-divided into six equal parts. A sample was then taken from each of these parts and spread out on a glass slide. Each sample was rinsed with Hertwitg liquid (Baumgartner and Martin 1939) and mounted with glycerin. All 6 of the preparations underwent an examination to determine the frequency of appearance

of the diet components in 20 different fields, obtained at 100 X under the microscope. Our aim was to select a sample of 10 stomachs per quarter year in order to determine the diet variation over the two-year study period. We also attempted to balance the presence of males and females. The identification of the remains was carried out by comparing a collection of microscopic preparations of plant epidermis.

Analysis of trophic diversity was done according to Ruiz (1985), who has developed methods based on the models of Hurtubia and Di Castri (1972), Hurtubia (1973) and Pielou (1966 a, b, 1975).

A matrix was prepared according to this method. Rows represented different types of food, and columns, the distinct variables: appearance frequency in number (N) and percentage (%N), percentage of stomachs with a specific type of food (%P) and Simpson's dominance ratio ($D = \Sigma Pi^2$)($1 < i < z$, z = total number of digestive tracts). Pi is the probability of a food unit from stomach i belonging to a certain type of food. $D' = D/z \times 100$ compares the different matrix indices. $D'' = D'/\Sigma D' \times 100$ expresses the value of D' as a percentage. The cumulative diversity curve Hz was drawn by arranging the stomachs according to their diversity in increasing or decreasing order. This was used to estimate the representativity of the sample studied. To calculate the diversity of the diet the Brillouin expression was used: $H = 1/N \times (\log_2 N! - \Sigma \log_2 N_i!)$. Brillouin's diversity index is recommended for the investigation of trophic diversity by various authors (Pielou 1966 a, b, 1975; Hurtubia 1973; Ruiz 1985). The value of Hz corresponded to the last value of the cumulative diversity function. $Hp = 1/(z-t)\,\Sigma\,hk$, ($t+1 < k < z$). $hk = (Mk \times Hk - Mk\text{-}1 \times Hk\text{-}1)/(Mk - Mk\text{-}1)$, Mk = number of prey of the k digestive tract, Hk = diversity of the k digestive tract, t = point at which Hk/k curve becomes stabilized. The average diversity values $\overline{H}$ and the equitability (E) were also compared.

The similarity between the diets of each season was estimated using Spearman's correlation coefficient. The diet of males and females was compared by means of the Kolmogorov-Smirnov and Spearman's correlation coefficient considering its greater proximity. The Chi-squared test was used to compare the green diet with its availability in the field.

The diet of *Microtus pyrenaicus* was studied using the analysis of 74 stomachs from individuals caught over a two year period of field work. This made it possible to identify a total of 4,881 particles belonging to 11 different food types.

Results

Diet composition

Figure 1 shows the cumulative diversity curves in which the stomachs are arranged according to their diversity in increasing or decreasing order. In the top curve, based on the

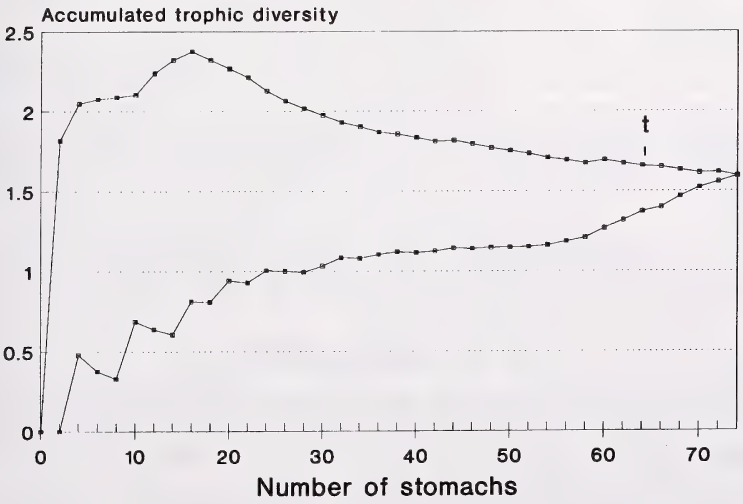


Fig. 1. Cumulative trophic diversity with stomachs arranged according to their diversity in increasing and decreasing order. Point t represents the tract from which the curve is considered stabilized (n = 74).

Table 1. Trophic matrix for the annual diet of *Microtus pyrenaicus* (n = 74).

	N	%N	P	D	D′	D″
Arthropods						
Adults	8	0.2	10.8	0.003	0.006	0.006
Lichens	274	0.5	1.3	0.34	0.46	0.73
Fungi	95	1.9	10.8	0.61	0.82	1.29
Mosses	30	0.6	12.2	0.04	0.06	0.09
A. v. p. Dicotiled.	2 896	59.3	95.9	33.18	44.84	70.19
A. v. p. Monocotil.	1 463	30.0	82.4	9.95	13.44	21.04
Floral parts	180	3.7	16.2	2.31	3.12	4.89
Pulpous fruits	39	0.8	2.7	0.24	0.32	0.51
Seed grasses	40	0.8	12.2	0.05	0.07	0.12
Seeds of *Fagus*	30	0.6	1.3	0.29	0.39	0.61
Roots	73	1.5	4.0	0.25	0.34	0.53

Table 2. Taxonomic groups of plants identified in the seasonal diet of *Microtus pyrenaicus.*

Autumn	Winter	Spring	Summer
Jasione montana	*Achillea millefolium*	*Stachys sylvatica*	*Prunella vulgaris*
Bellis perennis	*Potentilla erecta*	*Lamiastrum galeobdolon*	*Potentilla sterilis*
Hypochoeris radicata	*Potentilla* sp.	*Ranunculus nemorosus*	*Plantago* sp.
Lamium maculatum	*Lamiastrum galeobdolon*	*Ajuga reptans*	*Trifolium pratense*
Prunella vulgaris	*Ranunculus* sp.	*Ajuga* sp.	*Trifolium repens*
Ranunculus repens	*Plantago* sp.	*Stachys sylvatica*	*Trifolium reptans*
Stellaria uliginosa	*Trifolium* sp.	*Prunella vulgaris*	*Trifolium* sp.
Plantago lanceolata	Gramineae	*Plantago lanceolata*	Gramineae
Plantago sp.	*Anthoxantum odoratum*	*Plantago* sp.	*Carex* sp.
Trifolium reptans	*Carex* sp.	*Trifolium repens*	
Trifolium sp.		*Trifolium pratense*	
Gramineae		*Trifolium* sp.	
Cinosurus cristatus		Gramineae	
Poa pratensis			
Carex sp.			

accumulation of 62 stomachs, the graph is deemed to be sufficiently stabilized so as to consider that the sample is an accurate representation of the diet of the population in the area studied.

The most representative type of food in the diet consists of aerial vegetative parts (A. v. p.) of Dicotyledoneae (Tab. 1). Several species have been identified within this group (Tab. 2). The bulk of the diet is made up of the aerial vegetative parts of the Monocotyledoneae in addition to the above. A number of taxa have been identified in this group (Tab. 2). The remaining food types %N = 10.7 comprise: flowers (Leguminosae, Gen. *Trifolium*, Compositae and Gramineae have been found); bryophytes; fungi (in two stomachs identified as Ascomyceta, Gen. *Emericella*); herbaceous seeds; arthropods (in 3 cases identified as mites); radical parts; fleshy fruits (at least in one case belonging to *Rubus* sp.); *Fagus sylvatica* seeds and a small amount of lichens.

The trophic diversity values obtained in the sample studied are as follows: $\overline{H} = 0.783$ (E. S. = 0.046, n = 74), $H_p = 1.249$ (E. S. = 0.331, n = 12), $H_z = 1.595$, E = 0.445.

Table 3. A comparison of the seasonal diets using Spearman's range correlation test. Above the diagonal: correlation coefficients. Below the diagonal: significance levels.

	Aut. 1984	Win. 1985	Spr. 1985	Sum. 1985	Aut. 1985	Win. 1986	Spr. 1986	Sum. 1986
Aut. 1984		0.647	0.606	0.552	0.631	0.724	0,657	0,254
Win. 1985	0.041		0.783	0.645	0.400	0.447	0,481	0,292
Spr. 1985	0.055	0.013		0.719	0.636	0.499	0,782	0,254
Sum. 1985	0.081	0.041	0.023		0.418	0.356	0,760	0,465
Aut. 1985	0.046	0.206	0.044	0.186		0.599	0,673	0,264
Win. 1986	0.022	0.157	0.115	0.261	0.058		0,532	0,471
Spr. 1986	0.038	0.128	0.013	0.016	0.033	0.092		0,507
Sum. 1986	0.421	0.356	0.421	0.142	0.403	0.136	0,108	

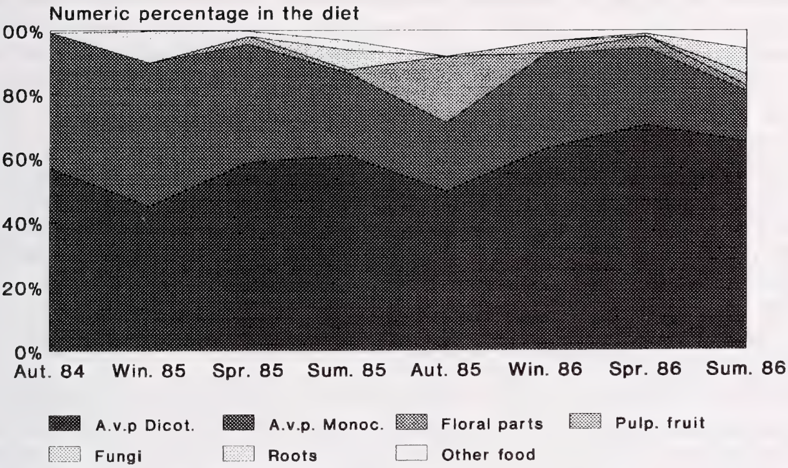


Fig. 2. Seasonal variation in the numerical percentage (N%) of the main types of food.

Seasonal variation in the diet

A comparison of the seasonal diets by means of the correlation index (Tab. 3) shows that the diet remains basically the same except during the two summers and one of the autumn periods (1985) when somewhat more individualized diets were observed. Throughout the two year study, the dicotyledons generally made up the largest proportion of the diet (Fig. 2). The monocotyledons, which appear in smaller percentages, were also a major food source during the study period. Overall, there appears to be a certain pattern in the abundance of green food, which reaches its peak in spring.

In summer and autumn of 1985 and the summer of 1986 the diet expanded to other types of food: fungi, flowers, fruits and seeds of herbaceous plants or beech trees.

Food selection

The green food consumed by *Microtus pyrenaicus* makes up 89.3% of the diet. Most of the green food components consist of dicotyledons (66.4%) and the remainder (33.6%) are monocotyledons. A comparison of the frequencies of these two components in terms of actual inclusion in the diet and the expected frequency based on field availability (53.5% monocotyledons and 46.5% dicotyledons) shows significant differences (Chi-squared = 2111.1, d. f. = 1, $p < 0.001$).

Diet comparison between sexes

Diets of males and females were compared using Spearman's correlation test with the following results: $r_s = 0.560$; $n = 11$; $p = 0.076$. The application of the Kolmogorov-Smirnov test resulted in a maximum estimated distance of DN = 0.182, p = 1.0. The following data refer to niche amplitude for each sex: Males: Number of stomachs studied = 35; Food Types = 9. $\overline{H} = 0.768$ (E. S. = 0.066, n = 35), $H_p = 0.953$ (E. S. = 0.037, n = 10), $H_z = 1.411$, E = 0.447. Females: Number stomachs studied = 39; Food Types = 11. $\overline{H} = 0.769$ (E. S. = 0.065, n = 39), $H_p = 1.537$ (E. S. = 0.322, n = 12), $H_z = 1.673$, E = 0.480.

Discussion

No references to the diet of *Microtus pyrenaicus* were found in the literature. Based on data collected in this study it may be concluded that the diet of this species is fundamentally herbaceous, consisting of the aerial green parts of pratal herbaceous plants, made up mostly of dicotyledons. The amplitude of the surface covered by the two diversity curves implies that there is some variation in the patterns of the trophic composition of the stomach contents which is linked to seasonal changes.

Although the number of food types consumed is relatively broad, the low cumulative diversity and equitability values reveal a diet that is specialized in very few resources. The population diversity value (H_p), which is markedly lower than that of cumulative diversity (H_z), also indicates that very few types of food are consumed with a noticeable predominance of anyone type.

On comparing the vegetative cover of monocotyledons and dicotyledons in the field with the ratio in which they appear in the diet, it is evident that the dicotyledons are chosen as the preferred food over monocotyledons.

Taking into account the annual variations in the diet in terms of the production in the herbaceous stratum (Castién 1994), we may conclude that grass makes up the largest part of the diet during spring, which coincides with the beginning of the vegetative period.

Arthropods are practically non-existent in the stomach. It is highly probable that the specimens that have been identified belong to external parasites of the animal itself.

Thus, it is possible to characterize *Microtus pyrenaicus* as a markedly folivorous species, which feeds primarily on dicotyledons, diversifying its diet during the summer by consuming small amounts of other non-green vegetative foods.

The cumulative diversity values and population diversity are slightly higher in females than in males. However, the standard deviation amplitude in the case of H_p does not allow to establish differences at the level of significance.

Acknowledgements

The authors would like to thank I. Leránoz (Pamplona), for his cooperation in the sample collection.

Zusammenfassung

Die Nahrung von Microtus pyrenaicus De Sélys-Longchamps, 1847 in den Westpyrenäen

Es wird über die Zusammensetzung der Nahrung von *Microtus pyrenaicus* nach Analysen von Mageninhalten berichtet. Ingesamt wurden 74 Mägen untersucht. Der Speisezettel der Art besteht in erster Linie aus oberirdischen vegetativen Teilen, sowohl von Dikotyledonen (59,3%) als auch von Monokotyledonen (30,0%). Blütenteile, Moose, Pilzen und Kräutersamen bilden den restlichen Anteil

(10%). Das ganze Jahr über ernährt sich die Art vorwiegend von grünen Pflanzenteilen, jedoch läßt sich im Sommer und Herbst eine größere Variation in der Zusammensetzung der Nahrung erkennen. Auf den Wiesen, die sie bewohnt, zieht *Microtus pyrenaicus* die Plätze mit Dikotyledonen-Bewuchs denen mit Monokotyledonen-Bewuchs vor. Aus den vorliegenden (niedrigen) Werten der Gleichmäßigkeit aber auch der kumulativen Diversität der Nahrungzusammensetzung läßt sich schließen, daß die Art stenophag ist.

References

Baumgartner, L. L.; Martin, A. C. (1939): Plant histology as an aid Squirrel food habit studies. J. Wild. Manage. **3**, 266–268.

Borghi, C. E.; Giannoni, S. M.; Martinez-Rica, J. P. (1994): Habitat segregation of three sympatric fossorial rodents in the Spanish Pyrenees. Z. Säugetierkunde **59**, 52–57.

Braun-Blanquet, J. (1967): Vegetationsskizzen aus dem Baskenland mit Ausblicken auf das weitere Ibero-Atlantikum. II. Vegetatio **14**, 1–126.

Butet, A. (1985): Méthode d'étude du régime alimentaire d'un rongeur polyphage (*Apodemus sylvaticus* L.) par l'analyse microscopique des fèces. Mammalia **49**, 455–483.

Castién, E. (1994): Estudio bioecológico de los micromamíferos (Insectivora y Rodentia) de un hayedo acidófilo. Quinto Real. Navarra Tesis Doctoral, Universidad de Barcelona.

Castién, E.; Gosálbez, J. (1995): Reproductive cycle of *Microtus pyrenaicus* De Sélys-Longchamps, 1847 (Mammalia, Rodentia) in the Western Pyrenees. Z. Säugetierkunde **60**, 170–175.

Gosálbez, J.; Ventura, J.; Götzens, G.; Escola, A. (1985): *Microtus pyrenaicus* (de Sélys-Longchamps, 1847) (Rodentia; Arvicolidae) en el NE ibérico. P. Dept. Zool. Barcelona **11**, 83–91.

Greigh-Smith, P. (1964): Quantitative plant ecology. London: Butterworths.

Hansson, L. (1970): Methods of morphological diet micro-analysis in rodents. Oikos **21**, 255–266.

Hurtubia, J. (1973): Trophic diversity measurement in sympatric predatory species. Ecology **54**, 885–890.

Hurtubia, J.; Di Castri, F. (1973): Segregation of lizard niches in the Mediterranean region of Chile. In: Mediterranean Type Ecosystems. Origin and Structure. Ed. by F. Di Castri and H. A. Mooney. New York: Springer-Verlag. Pp. 349–363.

Krapp, F. (1982): *Microtus pyrenaicus* (de Sélys-Longchamps, 1847) – Pyrenäen – Kleinwühlmaus In: Handbuch der Säugetiere Europas Vol. 2/I. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Akademische Verlagsges. Pp. 443–446.

Obrtel, R.; Holisova, V. (1976): Trophic diversity and dietary overlap of two sympatric rodents. Zool. Listy **25**, 217–227.

Pielou, E. C. (1966 a): Species-diversity and pattern-diversity in the study of ecological succesion. J. Theor. Biol. **10**, 370–383.

Pielou, E. C. (1966 b): The measurement of diversity in different types of biological collections. J. Theor. Biol. **13**, 131–144.

Pielou, E. C. (1975): Ecological diversity. New York: John Wiley and Sons.

Ruiz, X. (1985): An analysis of the diet of cattle egrets in the Ebro Delta, Spain. Ardea **73**, 49–60.

Saint-Girons, M. C.; Fayard, A.; Fons, R.; Libois, R.; Turpin, F. (1978): Les micromammiféres du versant Français des Pyrénées atlantiques. Bull. soc. Hist. nat. Toulouse **114**, 247–260.

Ventura, J.; Gosalbez, J.; Lopez-Fuster, M. J. (1989): Trophic ecology of *Arvicola sapidus* Miller, 1908 (Rodentia, Arvicolidae) in the Ebro Delta (Spain). Zool. Anz. **223**, 283–290.

Authors' addresses: Enrique Castién, Servicio de Conservación de la Naturaleza, Gobierno de Navarra, C./ Alhóndiga 1, E-31002 Pamplona and Joaquim Gosálbez, Departament de Biología Animal, Universitat de Barcelona, Avgda. Diagonal 645, E-08028 Barcelona, Spain.

Z. Säugetierkunde **62** (1997) 158–171

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Habitat fidelity and habitat utilization of an arboreal mammal (*Myoxus glis*) in two different forests

By W. Schlund, Friederike Scharfe, M. J. Stauss and J. F. Burkhardt

Behavioral Physiology, University of Tübingen, Tübingen, Germany

Receipt of Ms. 25. 06.1996
Acceptance of Ms. 26. 10. 1996

Abstract

In a long term study (1982–1994) nest box occupation by edible dormice was investigated in a deciduous and a coniferous-mixed forest. Within both forests edible dormice showed preference as well as avoidance of certain areas. Habitat fidelity was high since shifts between the forests (distance 1 km) was rare. Nest box fidelity was high as well, although higher for females and their daughters than for their sons, and higher in the deciduous, optimal forest than in the coniferous, suboptimal forest. In either forest nest box occupation was correlated with 19 habitat parameters on two spatial scales (900 m^2 and 8100 m^2 around each nest box). These correlations differed considerably between the forests but resulted in a similar interpretation: On the large scale, parameters associated with food availability (e. g. beeches, oaks) and predator avoidance (e. g. tree density, height of the nest box) were important for habitat utilization. On the small scale, habitat choice is less important.

Introduction

Animals live in environments, in which survival and successful reproduction is most likely guaranteed (e. g. Ims 1987; Ostfeld 1990). Their choice of habitats involves responses to patch structure at a series of hierarchical levels and one must consider more than a single scale of patchiness to understand its consequences (Hutto 1985; Wiens 1985; Morris 1987). Thus, it is important to consider spatial scale in studies of habitat associations because the various factors that affect a species may act at different spatial scales (Maurer 1985; Wiens 1986; Bock 1987; Kotliar and Wiens 1990; Orians and Wittenberger 1991; Lima and Zollner 1996).

The edible dormouse (*Myoxus glis* (L.)) is regarded as a species with widespread habitat demands. In Central Europe it is found from park-like landscapes to dense, mixed forests with coniferous and deciduous trees (Storch 1978; Bitz 1990). In general, preferred habitats are deciduous forests with oak trees and other hardwood species. In such habitats dormice show maximized reproductive success and have reached highest population densities (Storch 1978). In this study we investigate whether or not habitat utilization in edible dormice takes place at all and if so, on which spatial scale such a possible choice is made. In contrast to terrestrial voles and mice, arboreal edible dormice are somewhat more difficult to study. Fortunately, besides natural tree holes edible dormice also use artificial nest boxes for resting and rearing their young (see for example Löhrl 1955; v. Vietinghoff-Riesch 1960; Pilastro et al. 1994; Bieber 1995; Schlund 1996).

On two experimentally created scales, nest box occupation frequency of edible dormice was correlated with habitat parameters that were assumed to be important for maxi-

mizing fitness or reproductive success. The small scale encompasses the area directly around a nest box. Here, factors connected with the suitability of the rearing situation such as microclimate or the defendability of the rearing site might be important but also factors that affect survival like the ease of access to the nest box or exposure to predators. The large scale comprises an area that is approximately the size of the mean home range of edible dormice (Hönel 1991). Thus, in addition to the former factors, food availability and presence of competitors and predators at the feeding sites might be important. The described two scales are investigated within two separate forests of different general quality characteristics that influence morphology, survival, and reproduction of edible dormice (Schlund 1996). Insight into the processes of habitat selection can be gained by comparing patterns of habitat utilization by a single species in two habitats that differ in structure (Holmes 1981; Robinson and Holmes 1982). Furthermore, investigating scale effects allows us to distinguish choice hierarchies (Wiens et al. 1987) and thus broaden our understanding of mechanisms determining habitat utilization.

Material and methods

In a 13 year study (1982–1994) we recorded nest box occupation of edible dormice in two woodlands, a deciduous forest of approximately 8 hectars and a coniferous-mixed forest of about 12 hectars. The deciduous forest consists mainly of up to 150 year old tall beech and oak trees (70:20; 10% other tree species; forest management practice for tall branchless tree trunks), and a separate young tree stand with oak, beech and pine trees. The coniferous-mixed forest is more homogeneous with approximately 100 year old pine, spruce and beech trees (60:20:20) and with intermixed 20 year old spruce and beech trees (30:70). Both woodlands are located 1 km from each other within a forest area of 150 km^2 near Tübingen in south-west Germany (48°33′N, 9°00′E) (see Schlund et al. 1993). Nest boxes were spaced in a 30 m grid in both forests. Some of the nest boxes had small entry holes of 26 mm diameter that were not usable by edible dormice. Thus, only 80 of 88 (in the deciduous forest) and 91 of 124 (in the coniferous-mixed forest) nest boxes were suitable for occupation by edible dormice.

Nest box occupation was determined with the help of the typical leaf nests that are made for resting or giving birth and rearing young. Therefore nest box occupation does not reflect the real number of edible dormice because several animals may live in the nest box at the same time and in the course of a year.

In an area of 30×30 m around each nest box 19 habitat parameters were recorded: Number of trees (DBH > 7.5 cm) of the following tree species: beech *Fagus sylvatica* (BEE), oak *Quercus robur* and *Q. petraea* (OAK), pine *Pinus sylvestris* (PIN), spruce *Picea abies* (SPR), larch *Larix decidua* (LAR), other deciduous trees (OTR) like ash *Fraxinus excelsior*, lime *Tilia platyphyllos* or maple *Acer* sp. and fruit trees (FRT) like apple tree *Malus domestica*, pear tree *Pyrus communis* or cherry tree *Prunus avium*.

DIV: tree species diversity (Shannon-index; Mühlenberg 1989).

DEN: tree density per 30 x 30 m area.

AGE: age of the tree stand, estimated in five classes.

UST: understory cover (e. g. blackberry *Rubus fruticosus* and raspberry *Rubus idaeus*) [m^2].

YTR: number of young trees (DBH < 7.5 cm).

TST: number of tree stumps.

HDG: area of the forest edge with hedges [m^2].

OPA: open areas (without tree stands; e. g. farmland, meadow or paths) [m^2].

HIG: height of the nest box [cm].

CIR: circumference of the nest box tree measured at breast height [cm].

DIS: distance between the nest box tree and the nearest tree with DBH > 30 cm [m].

SUN: measurement of light influx during a 24 h period on top of the nest boxes using an ozalid light meter (Friend 1961; Glück 1979).

For further details see Schlund (1996). Statistical analysis was performed according to Sachs (1984) using the SAS (1987) software package for personal computers.

The two forests differed significantly in most habitat parameters (Tab. 1). Since many of the habitat parameters were highly correlated with each other, we additionally performed a Principal Component

Table 1. Means ($\bar{x}$) and standard deviations (s) of the habitat parameters of the studied areas. Comparison of the habitat parameters between the coniferous-mixed and the deciduous forest (Mann-Whitney-U-test (MWU); z-values and levels of significance (adjusted by applying the sequential Bonferroni test) are given with * = $p < 0.05$; ** = $p < 0.01$ and *** = $p < 0.001$, n = number of investigated grids). Abbreviations see Material and methods.

	deciduous forest $\bar{x} \pm s$ n = 88	coniferous-mixed forest $\bar{x} \pm s$ n = 124	MWU z	p
BEE	33.7 ± 17.4	17.9 ± 8.9	6.72	***
OAK	9.9 ± 8.7	0.1 ± 0.5	12.79	***
PIN	6.8 ± 12.0	13.5 ± 5.5	7.28	***
SPR	–	11.8 ± 8.7	–	–
LAR	1.5 ± 4.2	0.3 ± 0.7	0.62	n.s.
OTR	8.0 ± 18.7	0.4 ± 1.4	6.85	***
FRT	0.4 ± 1.0	0.0 ± 0.2	4.93	***
DIV	0.8 ± 0.3	1.0 ± 0.2	6.15	**
DEN	60.3 ± 26.1	44.0 ± 8.8	5.02	***
AGE	3.6 ± 1.1	4.2 ± 0.6	3.29	**
UST	4.1 ± 17.8	77.6 ± 113.9	6.95	***
YTR	12.1 ± 29.5	39.8 ± 39.0	9.19	**
TST	19.9 ± 11.2	20.1 ± 6.3	1.38	n.s.
HDG	12.1 ± 29.5	2.1 ± 11.6	3.01	**
OPA	10.1 ± 23.9	32.0 ± 54.4	3.37	**
HIG	310.7 ± 25.3	279.6 ± 28.9	8.15	***
CIR	84.8 ± 28.5	101.2 ± 37.4	3.21	**
DIS	2.4 ± 0.7	3.0 ± 1.4	6.45	***
SUN	4.8 ± 0.9	6.2 ± 0.4	7.31	***

Analysis (PCA) on the 19 parameters. Here, as well, the two investigated areas were clearly separated (Fig. 1). The deciduous forest was quite inhomogeneous with mainly old beech and oak trees and with young dense parts of the forest, with diverse tree stands, whereas the coniferous-mixed forest was very homogeneous with pine, spruce and beech trees of similar age.

Occupation frequency of nest boxes was standardized to the number of nest boxes per hectar in each study area. Both forests were then compared with respect to occupation frequency in those 13 years. Absolute differences (t-test for paired samples) as well as the correlation of the course of occupation frequencies between the two study areas were determined.

Two scales were experimentally created and analyzed in order to investigate which factors may play an important role in habitat use of edible dormice. In the small scale analysis the habitat parameters of every 30 × 30 m area (900 m^2) around each nest box were correlated (Spearman rank correlation) with occupation frequency over the 13 years in that central nest box. Correlations were considered significant if they corresponded to $p < 0.05$ after applying the sequential Bonferroni test (RICE 1989). In addition, we performed a Principal Component Analysis (PCA) on the parameters. A maximum of five axes were computed so that approximately two thirds of the variation was accounted for. These components

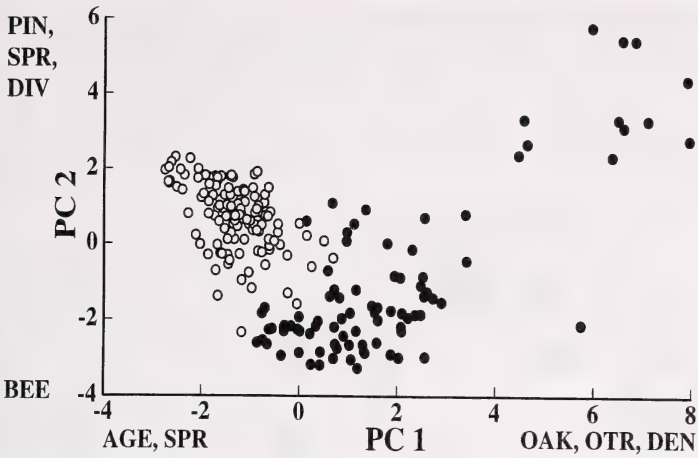


Fig. 1. Distribution of 171 nest box areas in a habitat space defined by the first two components of a PCA based on 19 habitat parameters; (●) deciduous forest, (○) coniferous-mixed forest.

were correlated with occupation frequency. In a separate analysis preference for nest box tree species as well as associated nest box parameters like diameter, height of the nest box and distance to the nearest tree were investigated with respect to occupation frequency. The large scale enclosing the area of 9 nest boxes (90×90 m = 8 100 m^2) corresponds to the mean territory size of edible dormice (Hönel 1991). Naturally, nest boxes situated at the edge of the study areas had fewer neighbouring nest boxes. Therefore we recorded the 19 habitat parameters for the corresponding 30×30 m adjacent areas (without nest boxes) to complete the 90×90 m area.

Occupation shifted frequently between adjacent nest boxes from year to year, therefore mean occupation frequency of all 9 nest boxes (or correspondingly fewer if nest boxes were not suitable for occupation or not present at the edges) was correlated with the mean habitat measurements of the 90×90 m area (significant correlations corresponding to $p < 0.05$ after applying the sequential Bonferroni test). In addition, mean occupation rate of the 9 adjacent nest boxes reveals more clearly whether an area was suited for rearing young than just the occupation frequency of the central nest box. Again a PCA was performed and the components were correlated with occupation frequency. The large scale encompasses the areas of 9 nest boxes but is referred to the corresponding central nest box. This enabled us to analyze both scales with equal sample sizes. As a consequence 6 of the 9 nest box areas overlap with every neighbouring large scale area.

In habitats differing considerably in vegetation structure choice might be made on a non-linear basis (e.g. Wiens 1992) or even in opposite directions. The distance between both woodlands is about 1 km (within a continuous forest) and since exchange between the investigated areas was extremely rare, the two woodlands were analyzed separately and choice patterns were subsequently compared.

In 1993 through 1995 nest boxes were checked once a week between May and October. Dormice were marked individually with passive integrated transponders (Schlund 1995), aged, weighed and sexed. Results of this study concerning morphology, population dynamics and reproduction are presented elsewhere (Schlund and Scharfe 1996). By using individual marking nest box constancy and home range fidelity of single dormice could be determined. Also nest box choice of females and subsequently of their offspring was monitored for several years. The year 1995 was not used for habitat preference analysis because selective logging took place in the winter 1994/1995, thus altering habitat structure considerably.

Results

Occupation frequencies in the 13 years (Fig. 2) were not random and differed from a Poisson distribution in both forests (Chi-square goodness of fit test: $\chi^2 = 304.61$, df = 8, $p < 0.001$ and $\chi^2 = 379.37$, df = 8, $p < 0.001$ for the coniferous-mixed forest and deciduous forest, respec-

tively). The Index of Dispersion (ID; LUDWIG and REYNOLDS 1988) indicated clumping (coniferous-mixed forest: ID = 4.08; deciduous forest: ID = 3.95). This shows that differential habitat occupation within both woodlands is due to non random processes.

The density of occupied nest boxes varied considerably throughout the 13 years in both forests ranging from 1.1 to 4.7 occupied nest boxes per hectar in the coniferous-mixed forest and from 0.8 to 4.0 per hectar in the deciduous forest (Fig. 3). The mean oc-

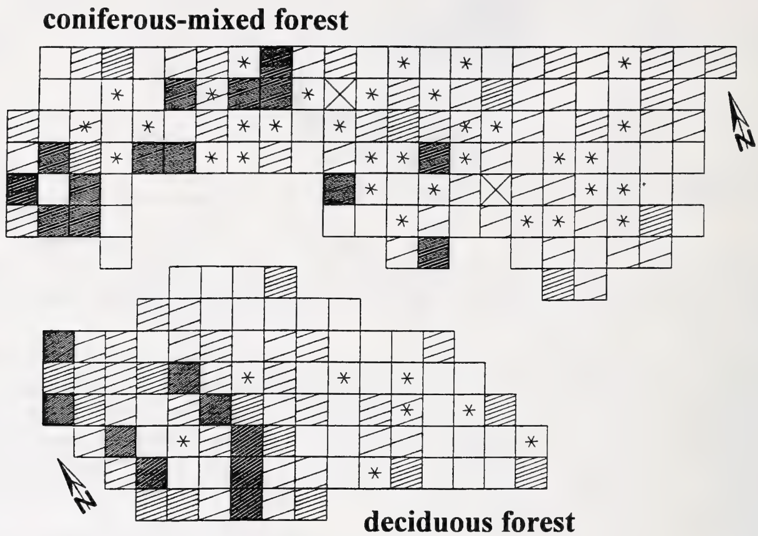


Fig. 2. Occupation frequency of nest boxes by edible dormice from 1982 to 1994 in the deciduous forest (n = 80 suitable nest boxes) and the coniferous forest (n = 91 suitable nest boxes). The nest boxes are spaced in a 30 m-grid.
□ = no occupation, ▨ = 1–3 occupations, ▨ = 4–6 occupations, ▨ = 7–9 occupations, ■ = >10 occupations. ⊡ = nest box with hole ≤26 mm, ☒ = area without nest box.

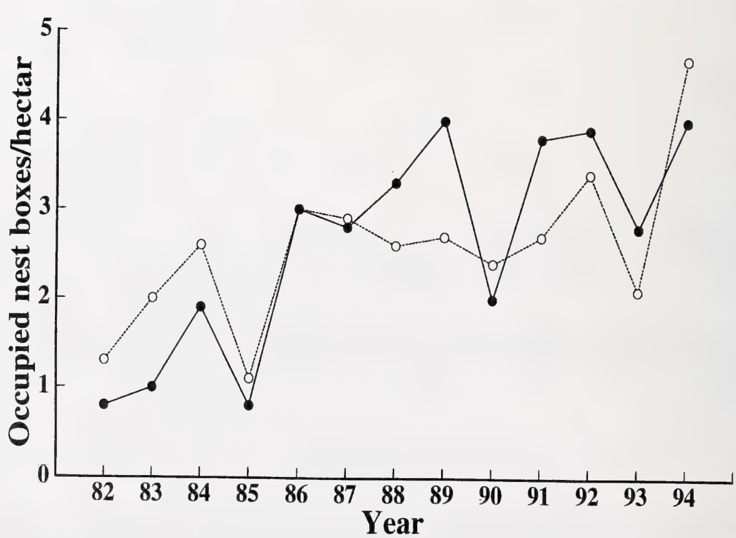


Fig. 3. Number of occupied nest boxes per ha from 1982 through 1994 in the deciduous (●) and coniferous-mixed forest (○).

cupation density did not differ between both habitats (t-test for paired samples: $t = 0.22$, $df = 12$, n. s.), and the course of occupation frequency in the 13 years correlated between the coniferous-mixed forest and the deciduous forest ($r_s = 0.83$, $df = 12$, $p < 0.001$).

Small scale; coniferous-mixed forest:

In the coniferous-mixed forest no significant correlation between nest box occupation frequency and the 19 habitat parameters was found (Tab. 2). Similarly, there was no significant correlation between nest box occupation and any of the PC-axes. 40 out of 91 nest box trees were beeches (44%), pine and spruce trees represented 31% and 24%, respectively. Nest boxes on beeches were occupied significantly above mean occupation frequency, whereas nest boxes on spruce trees were avoided (Fig. 4). The height of the nest boxes attached to beeches correlated positively with occupation frequency ($r_s = 0.42$, $N = 40$, $p < 0.008$). Height of the nest boxes attached to spruce and pine, however, did not correlate significantly ($r_s = 0.07$ and -0.25, respectively).

Large scale; coniferous-mixed forest:

Correlation of the large scale habitat variables with mean occupation frequency of the central nest box and its surrounding 8 nest boxes revealed a significant preference for nest boxes at greater heights with large circumference and a negative correlation with understory cover and tree stumps (Tab. 2).

The first 5 PC-axes accounted for 70.0% of the variation. The significant axes correlating with occupation frequency are shown in figure 4. Correlation with the second axis (accounting for 14.7% of the variation) described a significant positive association ($p < 0.03$) for beech trees and avoidance of understory cover and sun exposure. The fifth axis (only 8.3%) revealed the preference for nest boxes at greater heights and sun exposure ($p < 0.0001$).

Table 2. Spearman rank correlations between the 19 habitat parameters and the occupation frequency of edible dormice for both the small and the large scale of the investigated forests. Levels of significance were adjusted by applying the sequential Bonferroni test (see Material and methods). (*) = $p \leq 0.10$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	coniferous-mixed forest		deciduous forest	
	small scale r_s	large scale r_s	small scale r_s	large scale r_s
BEE	0.06	0.12	–0.13	0.02
OAK	0.02	0.24	0.13	0.50**
PIN	–0.05	0.17	0.29	0.70**
SPR	–0.17	–0.20	–	0.40**
LAR	–0.05	–0.01	0.08	0.59**
OTR	–0.02	0.08	0.38**	0.58**
FRT	0.06	0.10	–0.03	–0.18
DIV	0.00	0.02	0.46**	0.76**
DEN	–0.14	0.13	0.21	0.60**
AGE	–0.13	–0.18	–0.43**	–0.50**
UST	–0.15	–0.56**	0.14	–0.05
YTR	0.10	0.17	0.26	0.17
TST	–0.16	–0.37**	0.27	0.77**
HDG	0.00	–0.07	–0.05	–0.38**
OPA	0.12	–0.09	0.05	–0.27
HIG	0.07	0.46**	–0.08	0.06
CIR	–0.07	0.43**	–0.07	–0.24
DIS	–0.17	0.10	0.16	0.33*
SUN	–0.14	0.27	–0.30(*)	–0.59**

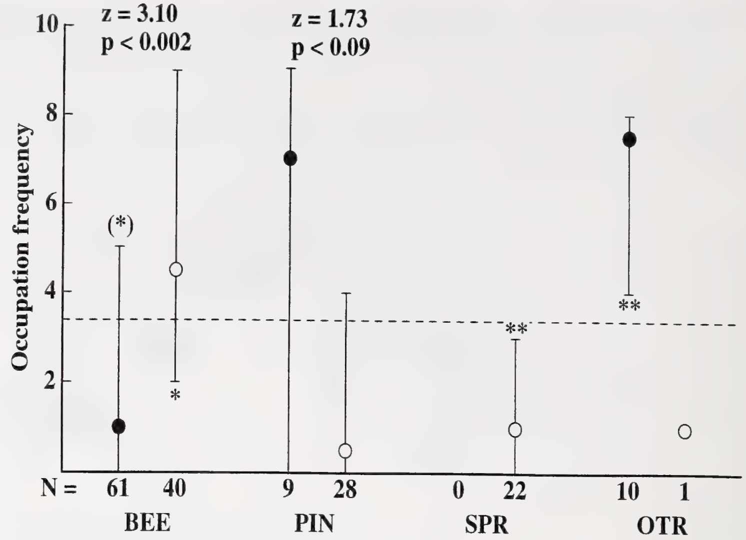


Fig. 4. Occupation frequency of nest boxes (median and quartiles) attached to different tree species in the deciduous (●) and coniferous-mixed forest (○). The dashed line shows mean occupation frequency per nest box. Tests between forests are Mann-Whitney-U and difference from mean occupation frequency are t-test or signed rank test (SAS 1987). For abbreviations see Material and methods.
(*) = $p \leq 0.1$; * = $p < 0.05$; ** = $p < 0.01$.

Small scale; deciduous forest:

In the deciduous forest correlations between nest box occupation frequency and habitat parameters revealed a significant preference for other trees and high tree diversity. Old tree stands and nest boxes with high sun exposure were avoided (Tab. 2).

The first 5 PC-axes accounted for 61.5% of the variation. The first axis (28.9%) and the fifth axis (6.4%) describing nest box parameters correlated significantly with occupation frequency (Fig. 6). In the first axis pine trees, larch trees, other trees, high tree diversity and density were preferred, whereas old tree stands were avoided ($p < 0.0001$). In the fifth axis, however, fruit trees and nest boxes with high sun exposure were avoided and understory cover was preferred ($p < 0.006$; Fig. 6). 61 of 80 nest boxes were attached to beech trees (76%), 11% of the nest box trees were pines and 13% were other trees. Nest boxes on beeches were occupied below mean occupation frequency, whereas nest boxes

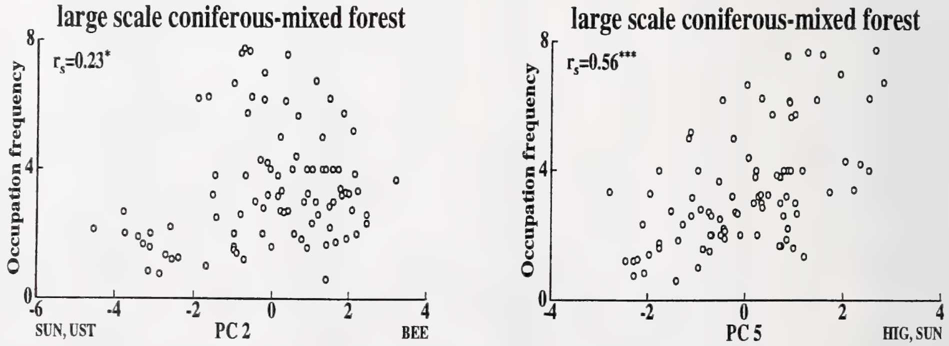


Fig. 5. Nest box occupation in relation to PC-axis 2 and PC-axis 5 in the large scale analysis of the coniferous-mixed forest. For abbreviations see Material and methods.

on other trees were significantly preferred (Fig. 4). The height of the nest boxes attached to beeches did not correlate with occupation frequency ($r_s = -0.19$). The same is true for pine ($r_s = 0.02$) and other trees ($r_s = 0.46$).

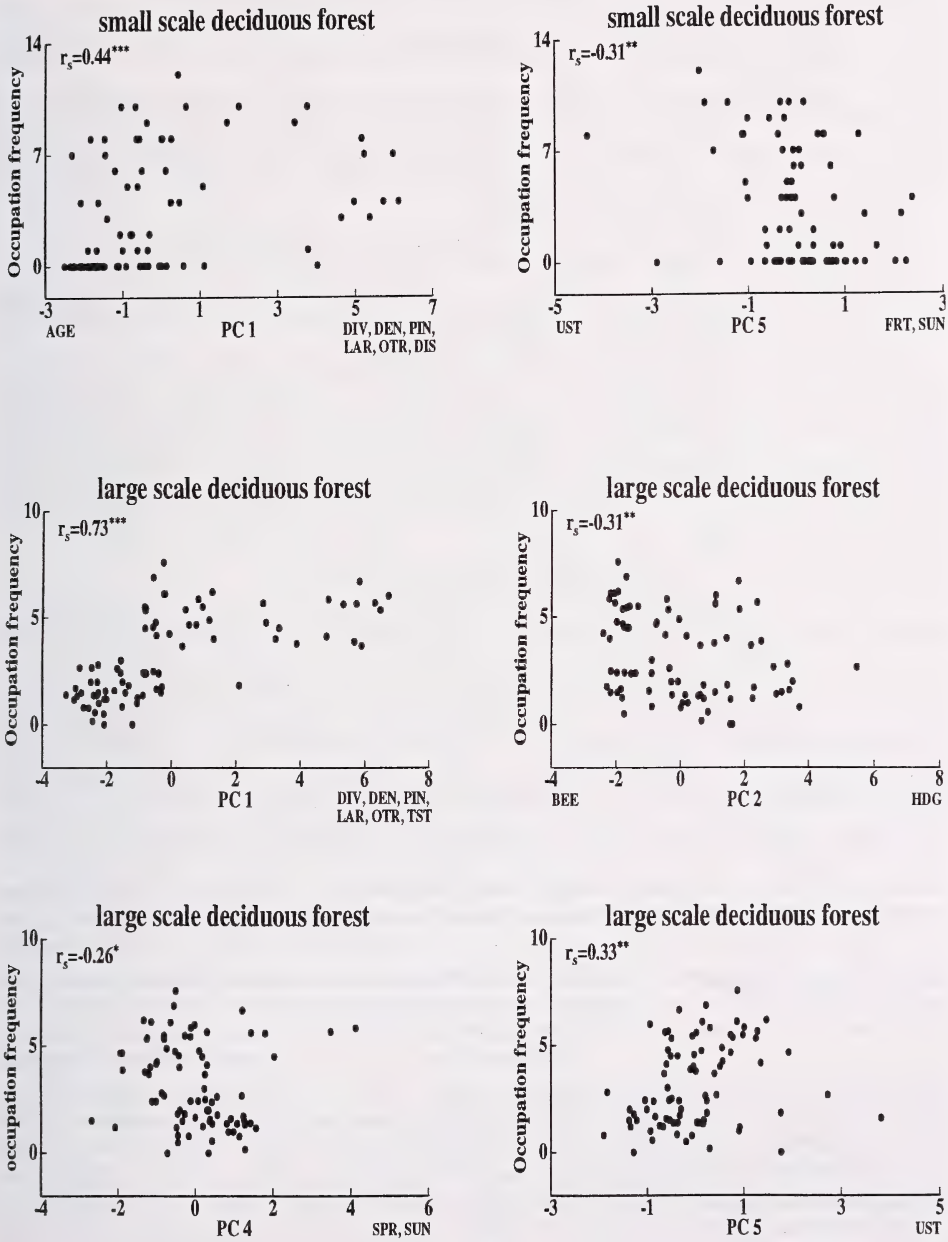


Fig. 6. Nest box occupation frequency in relation to PC-axis 1 and PC-axis 5 in the small scale analysis of the deciduous forest and in relation to PC-axes 1, 2, 4, and 5 in the large scale analysis of the deciduous forest. For abbreviations see Material and methods.

Large scale; deciduous forest:

In the large scale analysis areas with high tree diversity along with oak trees, pine trees, spruce trees, larch trees and other trees, high tree density and tree stumps showed positive correlations with mean occupation frequency, whereas old tree stands, nest boxes with high sun exposure and forest edge were negatively correlated (Tab. 2).

The first five PC-axes accounted for 81.4% of the variation. PC-axes 1, 2, 4 and 5 correlated significantly with nest box occupation (Fig. 6). The first axis (38.2%) describing high tree diversity with pine trees, larch trees and other trees and tree stands with high density, correlated positively. Moreover, areas with tree stumps were preferred ($p < 0.0001$). The second axis (18.0%) is characterized by preference for beech trees whereas forest edge was avoided ($p < 0.006$). In axis 4 (6.9%) spruce trees and nest boxes with high sun exposure were avoided ($p < 0.03$) and in axis 5 (5.1%) areas with a marked understory cover were preferred ($p < 0.003$).

Site fidelity and choice of nest boxes of individually marked animals:

From 1993 to 1995 more than 400 animals were marked in both forests. In 1993 not a single juvenile was observed in any of the two woodlands. Possible reasons for this complete absence of reproduction are discussed by Bieber (1995) and Schlund (1996). In 1994 and 1995, however, the dormice did reproduce.

Emigration rates/death rates amounted to more than 50% in both forests between 1993 and 1994 (deciduous (dec): 64.2%; coniferous-mixed (con): 50.8%) and to more than 70% between 1994 and 1995, respectively (dec: 71.1%; con: 71.2%). In three years only 2 dormice migrated between the two woodlands (1 from dec to con, 1 vice versa). In 1995 the retrapping rate of juveniles born in 1994 was more than 25% in both woodlands (dec: 26.9%; con: 25.6%) and did not differ significantly from retrapping rates of adult dormice (31% in both woodlands; dec: $\chi^2 = 0.44$, df =1, n. s.; con: $\chi^2 = 0.43$, df = 1, n. s.). This indicates a preference for the woodland in which an animal was born.

Strong site fidelity becomes apparent by analysing nest box choice of gestating females in 1994 and 1995. Occupation rate of the nest boxes in which the females gave birth (dec: 41 females; con: 31 females) correlated with the number of nest boxes occupied in the last 13 years in both forests (dec: $r_s = 0.43$, $p < 0.002$, $n = 49$; con: $r_s = 0.25$, $p < 0.05$, $n = 65$). Furthermore out of 7 females that gave birth both in 1994 and 1995 in the deciduous forest, 5 did so in the same nest box and 2 changed to neighbouring nest boxes (distance 30 m). Likewise, in the coniferous-mixed forest 6 out of 8 females remained in the same nest box, 1 occupied the directly neighbouring nest box and 1 stayed in the near vicinity (67 m). Even the offspring of 1994 were still recorded close to their natal nest boxes in the following year. In the deciduous forest the mean distance was 61 m (n = 15), in the coniferous-mixed forest it amounted to 157 m (n = 6). The difference between forests as well as the difference between sexes was highly significant (Tab. 3), the

Table 3. Mean distance [m] between natal nest box (1994) and nest boxes where the sons and daughters were encountered in 1995.

	deciduous forest				coniferous-mixed forest			
	$\bar{x}$	Min	Max	n	$\bar{x}$	Min	Max	n
sons	106	60	160	5	321	162	480	2
daughters	38	0	133	10	75	0	154	4
2-way analysis of variance		F				p		
model		8.53				0.002		
woodland		11.41				0.004		
sex		17.66				0.0006		
woodland * sex		5.70				0.03		

daughters occurring consistently closer to their natal nest boxes than the sons. Daughters that became mothers in their first year, however, were found at similar distances as non-reproductive daughters (dec: mothers $\bar{x} = 44$ m, n = 4; non-mothers $\bar{x} = 35$ m, n = 6; t-test: t = 0.3, n. s.; con: mothers $\bar{x} = 100$ m, n = 3; non-mother $\bar{x} = 0$ m, n = 1, no test).

Discussion

In this long term study on nest box occupation by edible dormice we showed that the number of occupied nest boxes throughout 13 years was similar in both investigated woodlands, a deciduous and a coniferous-mixed forest. This does not agree with other studies reporting on deciduous forests as optimal habitats for this small mammal species being inhabited by more dormice than coniferous forests (Storch 1978; Hönel 1991). However, a three year study (1993 through 1995) in the two forests on individually tagged edible dormice (passive integrated transponder) revealed a higher population density in the deciduous forest (Schlund 1996). Reasons for this discrepancy are: at first, one single nest box with a characteristic leaf nest may be occupied by up to 9 dormice (our own observation), secondly, other dormice may live in natural tree holes that are probably more common in the deciduous than in the coniferous-mixed forest. This means that the number of occupied nest boxes does not reflect population density. However, as this study shows, the analysis of occupied nest boxes through 13 years is sufficient to make statements on habitat utilization. Furthermore, frequently occupied nest boxes correlate with those nest boxes that are chosen for rearing young.

Habitat and site fidelity

Throughout the investigated 13 years the proportion of occupied nest boxes between the two forests remained relatively constant. Even in years with low density the coniferous-mixed forest was not vacated in favour of the better habitat. The forests are only 1 km apart and our radio-telemetry studies showed nightly ranges of dormice to the extent of more than 1 000 m (unpubl. data). Nevertheless exchange between the investigated areas was extremely rare. Thus, choice for woodlands is not made by assessing ad hoc qualities, although the perceptual range of dormice seems sufficiently large (see Lima and Zollner 1996). Forest utilization might be a result of tradition. A further indication is the high number of dormice being born and staying in the area where they have been raised (e. g. habitat preference in mice as a function of prior experience, Anderson 1973). This habitat fidelity is surprising since habitat quality even influences the condition of dormice. In the deciduous forest adult animals had higher body mass and larger body sizes, and reproductive output was significantly higher than in the coniferous mixed-tree forest (Schlund 1996; Schlund and Scharfe 1996). Comparable results of optimal habitats influencing the fitness of animals are reported in studies on white-footed mice (Wolff 1993) and red squirrels (Wauters and Dhondt 1989) and are explained by the authors with the more favourable food situation.

In addition, in either forest certain nest box areas were occupied more frequently than others, revealing a clumped dispersion. This strongly indicates that within both forests some areas were more suitable to edible dormice than others. The majority of occupied nest boxes were used for more than 8 years. Since the average life expectancy of dormice in the wild is 3 to 4 years (Bieber 1995) preferences for specific areas exist over generations of animals. Contrary to Pilastro (1992) we never found communal nesting in breeding females. However, we could demonstrate that female kin tend to stay and give birth in their natal nest box or in close vicinity.

Further aspects refer to sex and habitat specific dispersal differences. In both forests

females stay closer to their natal nest box than their brothers suggesting male dispersion (a common behaviour in mammals; Greenwood 1980; e. g. Goundie and Vessey 1986). In the coniferous-mixed forest both male and female offspring are found at greater distance from their birth place than in the deciduous forest. This may be due to differences in habitat quality and therefore divergent food resources of the two forests. The low quality coniferous-mixed forest might induce an expansion in individual foraging range, or wider dispersal to favourable but patchily distributed feeding areas (Wauters et al. 1995; see also Winker et al. 1995).

Habitat utilization

Correlations between nest box occupation and habitat parameters differed considerably between the two forests. Corresponding to these differences in habitat characteristics, completely different parameters were obviously important for the utilization of the optimal habitat. Hence, edible dormice followed no rigid choice pattern.

As a result of the strong site fidelity of edible dormice we might have expected that dormice exhibit habitat preferences on the small scale, meaning the areas directly around a nest box (900 m^2). However, on the level of the small scale habitat choice seems to play a secondary role. In the coniferous-mixed forest edible dormice did not show preferences for any of the habitat parameters. The choice for nest box trees, however, was clearly a choice for beeches. In a forest consisting mainly of pine and spruce, this could be interpreted as a behavioural reaction of an animal that is mostly attached to deciduous trees. In the deciduous forest beeches as nest box trees were rather avoided whereas other deciduous tree species were selected. A fact that might be attributed to the smooth and slippery bark of old beeches with large circumference, where dormice might easily slip and fall (Löhrl 1960; v. Vietinghoff-Riesch 1960; Schoppe 1975). This is in contrast to the coniferous-mixed forest where beeches are younger with smaller circumferences and branches growing lower at the tree trunk and are thus easier to climb. Furthermore, in the small scale analysis of the deciduous forest, preferences for few habitat parameters occurred. The importance of these parameters is elucidated on the large scale analysis.

Edible dormice live predominantly on a vegetarian diet consisting mainly of leaves in the early summer and fruits rich in protein and edible (e. g. oak and beech trees) in the autumn (v. Vietinghoff-Riesch 1960; Storch 1978). This accounts for the finding that on the large scale (8 100 m^2) the animals are found in areas with rich food sources meaning areas with oak trees and beech trees. Furthermore, in the deciduous forest they utilized areas with high tree diversity. Tree species like ash, lime or maple as well as pine and larch are an important enrichment in diet (Eiberle 1977; Hönel 1991; Kulzer et al. 1993). In the coniferous-mixed forest deciduous tree species were extremely rare with the exception of beech trees. Therefore beeches were preferred. Taking this relatively unbalanced diet of beeches into consideration, it seems surprising that edible dormice avoided nest box areas with a marked understory cover that consisted mainly of blackberries and raspberries. As our telemetry studies showed (unpublished work), dormice did indeed feed on blackberries and raspberries. However, since nest box areas with a high proportion of beech trees were preferred and since those correlated with low sun exposure on the ground, understory cover was not developed there.

Besides food availability predator avoidance may explain differences in habitat utilization. Both investigated forests are hunting grounds of the tawny owl (*Strix aluco* L.). This species catches its prey preferably in flight e. g. dormice while they are foraging in the tree crown. Dense areas provide the best protection against this predator (see Bezzel 1985). In the heterogeneous deciduous forest where dense young tree stands alternate with old and open areas edible dormice preferred indeed the denser tree stands. This is

not true for the coniferous-mixed forest. In this more homogeneous forest dense stands of deciduous tree species are nearly non existent, with the exception of stands of spruce trees which, however, are avoided.

Further protection against the tawny owl may be given by nest boxes fixed higher up on trees reducing the exposed and thus risky way between nest box and foraging place in the tree crown. In the coniferous-mixed forest nest boxes attached higher up were preferred. In the deciduous forest a comparable behaviour does not seem to exist. Here, height of the nest box does not correlate with occupation frequency. This is attributed to the tall beeches which account for 76% of the nest box trees. Here branches providing footholds or protection to the dormice on their long way (up to 15 m) to and from the tree crown do not exist. Thus a reduction of the distance between nest box and tree crown by a maximum of 1 m can not reduce the risk of predation or of slipping. This even forced the dormice to enter their nest boxes via neighbouring bushes or the ground (pers. observ.). In the coniferous-mixed forest the distance between nest box and tree crown is smaller and branches are found all the way down to the nest box, a result of different forest management.

Cats often catch edible dormice, as many residents of Hagelloch, the village bordering directly on the deciduous forest, reported. This hunting success is facilitated by dormice using the ground to access nest boxes at beech trees. Furthermore the abundance of cats from the nearby village might be a reason why dormice avoid the forest edge in the deciduous forest. This is a completely contrary result to an other study that has shown preferences of edible dormice for forest edges (Bieber 1995) due to a higher quality e. g. higher availability of food resources than inside the forest. In our investigation area, however, the food supply is guaranteed by intense fructification of many old oak trees and beech trees in the forest interior. In contrast, in the coniferous-mixed forest without adjacent settlement of men we found no avoidance of the forest edge. No positive edge effect could be observed, either. This might be due to less marked forest edges with only few and sparsely grown hedges.

Acknowledgements

We thank K. Schmidt-Koenig, J. U. Ganzhorn, for their helpful comments. Thanks are due to many helpers during our field work.

Zusammenfassung

Habitattreue und Habitatnutzung von Siebenschläfern, Myoxus glis (L.), in zwei unterschiedlichen Wäldern

In einem Laubwald und einem Nadel-Laubmischwald wurden über 13 Jahre (1982–1994) Nistkastenbelegungen durch Siebenschläfer untersucht. In beiden Waldgebieten gab es Areale, die von Siebenschläfern bevorzugt, andere dagegen gemieden wurden. Nur wenige Tiere wechselten zwischen den Gebieten, obwohl diese nur einen Kilometer auseinander lagen. Auch innerhalb der Waldgebiete war die Standorttreue der Siebenschläfer um bestimmte Nistkästen hoch, wobei im Laubwald die Nistkastentreue höher als im Nadel-Laubmischwald war. Außerdem zeigten Mütter und ihre Töchter höhere Nistkastentreue als Männchen. In beiden Waldgebieten wurden auf zwei räumlich unterschiedlichen Maßstäben (900 m^2 und 8 100 m^2 um jeden Nistkasten) die Nistkastenbelegungen mit 19 Habitatvariablen korreliert. Diese Korrelationen unterschieden sich zwischen den Waldgebieten erheblich, führten aber in beiden Gebieten zum gleichen Resultat: Auf der Ebene des großen Maßstabs waren Faktoren zur Nahrungssuche (z. B. Buchen, Eichen) und zum Prädationsschutz (z. B. Baumdichte, Nistkastenhöhe) wichtig. Auf der Ebene des kleinen Maßstabs spielte die Habitatwahl der Siebenschläfer nur eine untergeordnete Rolle.

References

ANDERSON, L. T. (1973): An analysis of habitat preference in mice as a function of prior experience. Behaviour **47**, 302–339.

BEZZEL, E. (1985): Kompendium der Vögel Mitteleuropas: Nonpasseriformes – Nichtsingvögel. Wiesbaden: Aula Verlag.

BIEBER, C. (1995): Ökologische Untersuchungen zur Populationsstruktur und -dynamik sowie zur Reproduktionsbiologie an drei Subpopulationen des Siebenschläfers (*Myoxus glis* L.). Diss. Philipps-Universität Marburg.

BITZ, A. (1990): Der Siebenschläfer *Glis glis* (Linnaeus, 1766), Familie Schlafmäuse (Gliridae). Mz. naturwiss. Arch., Beih. **13**, 299–321.

BOCK, C. E. (1987): Distribution-abundance relationships of some Arizona land birds: a matter of scale? Ecology **68**, 124–129.

EIBERLE, K. (1977): Zur Populationsdynamik des Siebenschläfers (*Glis glis* L.) im Lehrwald der ETHZ. Schweiz. Z. Forstwesen **128**, 630–645.

FRIEND, D. T. C. (1961): A simple method of measuring integrated light values in the field. Ecology **42**, 577–580.

GLÜCK, E. (1979): Abhängigkeit des Bruterfolges von der Lichtmenge am Neststandort. J. Orn. **120**, 215–220.

GOUNDIE T. R; VESSEY, S. H. (1986): Survival and dispersal of young white-footed mice born in nest boxes. J. Mammalogy **67**, 53–60.

GREENWOOD, P. J. (1980): Mating systems, philopatry and dispersal in birds and mammals. Anim. Behav. **28**, 1140–1162.

HOLMES, R. T. (1981): Theoretical aspects of habitat uses by birds. In: The use of multivariate statistics in studies of wildlife habitat. Ed. by D. E. CAPEN. U.S.D.A. Forest Service General Technical Report RM-**87**, 33–37.

HÖNEL, B. (1991): Raumnutzung und Sozialsystem freilebender Siebenschläfer (*Glis glis* L.). Diss. Universität Karlsruhe.

HUTTO, R. L. (1985): Habitat selection by non-breeding migratory land birds. In: Habitat selection in birds. Ed. by M. L. CODY. Orlando: Academic Press. Pp. 455–476.

IMS, R. A. (1987): Male spacing systems in microtine rodents. Am. Nat. **130**, 475–484.

KOTLIAR, N. B.; WIENS, J. A. (1990): Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. Oikos **59**, 253–260.

KULZER, E.; LINDEINER-WILDAU A. VON; WOLTERS, I. M. (1993): Säugetiere im Naturpark Schönbuch – Übersicht über die Biologie der Arten und Ergebnisse einer faunistisch-ökologischen Untersuchung in den Jahren 1989–1991. Karlsruhe: Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ. **71**.

LIMA, S. L.; ZOLLNER, P. A. (1996): Towards a behavioral ecology of ecological landscapes. TREE **11**, 131–135.

LÖHRL, H. (1955): Vermehrungsausfall beim Siebenschläfer, *Glis glis glis* (Linné, 1758), im Jahre 1954. Säugetierkundl. Mitt. **3**, 177.

LÖHRL, H. (1960): Säugetiere als Nisthöhlenbewohner in Südwestdeutschland mit Bemerkungen über ihre Biologie. Z. Säugetierkunde **25**, 66–73.

LUDWIG, J. A.; REYNOLDS, J. F. (1988): Statistical ecology. New York, Chichester: John Wiley and Sons.

MAURER, B. A. (1985): Avian community dynamics in desert grassland: observational scale and hierarchical structure. Ecol. Monogr. **55**, 295–312.

MORRIS, D. W. (1987): Ecological scale and habitat use. Ecology **68**, 362–369.

MÜHLENBERG, M. (1989): Freilandökologie. 2. Aufl. Heidelberg, Wiesbaden: Quelle und Meyer Verlag.

ORIANS, G.; WITTENBERGER, J. (1991): Spatial and temporal scales and habitat selection. Am. Nat. **137** (S), S 29–S 49.

OSTFELD, R. S. (1990): The ecology of territoriality in small mammals. TREE **5**, 411–415.

PILASTRO, A. (1992): Communal nesting between breeding females in a free-living population of fat dormouse (*Glis glis* L.). Boll. Zool. **59**, 63–68.

PILASTRO, A.; GOMIERO, T.; MARIN, G. (1994): Factors affecting body mass of young fat dormice (*Glis glis*) at weaning and by hibernation. J. Zool. (London) **234**, 13–23.

RICE, W. R. (1989): Analyzing tables of statistical tests. Evolution **43**, 223–225.

ROBINSON, S. K.; HOLMES, R. T. (1982): Foraging behavior of forest birds: the relationships among search tactics, diet, and habitat structure. Ecology **63**, 1918–1931.

SACHS, L. (1984): Angewandte Statistik. 6. Aufl. Berlin, Heidelberg: Springer Verlag.

SAS INSTITUTE (1987): SAS/STAT Guide for Personal Computers. Version 6 Edition, Cary, North Carolina.

SCHLUND, W. (1995): Individualmarkierung und Populationsbeobachtungen bei Siebenschläfern mit Hilfe von Transpondern. In: Methoden feldökologischer Säugetierforschung **1**. Ed. by M. STUBBE; A. STUBBE, and D. HEIDECKE. Halle–Wittenberg: Wissenschaftliche Beiträge/Martin-Luther-Universität, Pp. 345–354.

SCHLUND, W. (1996): Vergleich von Siebenschläferpopulationen (*Myoxus glis* L.) in zwei unterschiedlichen Waldgebieten. Diss. Eberhard-Karls-Universität Tübingen.

SCHLUND, W.; SCHARFE, F. (1996): Unterschiede zweier Siebenschläferpopulationen (*Myoxus glis* L.) im Schönbuch in Abhängigkeit des Lebensraumes. Veröff. Naturschutz Landschaftspflege Bad.-Württ. **71/72** (in press).

SCHLUND, W.; STAUSS, M. J.; BURKHARDT, J. F. (1993): Siebenschläfer in Nistkästen – eine Langzeitstudie zur Habitatwahl. Carolinea **51**, 93–100.

SCHOPPE, R (1975): Bemerkungen zur Verbreitung des Siebenschläfers im Raum Hildesheim. Beitr. Naturkunde Niedersachsens **28**, 67–72.

STORCH, G. (1978): Familie Gliridae Thomas, 1897 – Schläfer. In: Handbuch der Säugetiere Europas. Bd. 1 Nagetiere I. Ed. by J. NIETHAMMER and F. KRAPP. Wiesbaden: Akad. Verlagsges. Pp. 201–280.

VIETINGHOFF-RIESCH, A. FRHR. VON (1960): Der Siebenschläfer (*Glis glis* L.). Monographien der Wildsäugetiere Bd. 14. Ed. by D. MÜLLER-USING. Jena: Gustav Fischer Verlag.

WAUTERS, L. A.; DHONDT, A. A. (1989): Variation in length and body weight of the red squirrel (*Sciurus vulgaris*) in two different habitats. J. Zool. (London) **217**, 93–106.

WAUTERS, L. A.; LENS, L.; DHONDT, A. A. (1995): Variation in territory fidelity and territory shifts among red squirrel, *Sciurus vulgaris*, females. Anim. Behav. **49**, 187–193.

WIENS, J. A. (1985): Habitat selection in variable environments: shrubsteppe birds. In: Habitat selection in birds. Ed. by M. L. CODY. Orlando: Academic Press. Pp. 227–251.

WIENS, J. A. (1986): Spatial scale and temporal variation in studies of shrubsteppe birds. In: Community Ecology. Ed. by J. DIAMOND and T. J. CASE. New York: Harper and Row. Pp. 154–172.

WIENS, J. A. (1992): The Ecology of Bird Communities: Vol. 1. Foundations and patterns. Cambridge: Cambridge Univ. Press.

WIENS, J. A.; ROTENBERRY, J. T.; VAN HORNE, B. (1987): Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos **48**, 132–147.

WINKER, K.; RAPPOLE, J. H.; RAMOS, M. A. (1995): The use of movement data as an assay of habitat quality. Oecologia **101**, 211–216.

WOLFF, J. O. (1993): Does the "chitty effect" occur in *Peromyscus*? J. Mammalogy **74**, 846–851.

Authors' addresses: Dr. W. SCHLUND, FRIEDERIKE SCHARFE, M. J. STAUSS, Dr. J. F. BURKHARDT, Behavioral Physiology, University of Tübingen, Beim Kupferhammer 8, D-72070 Tübingen, Germany

Z. Säugetierkunde **62** (1997) 172–178

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Allozyme differentiation and systematic relationship of Zambian Giant mole-rats, *Cryptomys mechowi* (Bathyergidae, Rodentia)

By Maria G. Filippucci, M. Kawalika, M. Macholan, A. Scharff, and H. Burda

Department of Biology, University of Roma "Tor Vergata", Roma, Italy; Laboratory Section, Ndola City Council, Ndola, Zambia, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, Brno, Czech Republic; Department of General Zoology, Faculty of Biology, University of Essen, Essen, Germany

Receipt of Ms. 29. 05. 1996
Acceptance of Ms. 19. 06. 1996

Abstract

Allozymic variation encoded by 31 gene loci was studied in giant mole-rats (*Cryptomys mechowi*) and two species of common mole-rats from Zambia, and allozymic diversity encoded by 22 loci was re-analysed in *Cryptomys damarensis*, *C. h. hottentotus*, and *C. h. natalensis* from South Africa. The Zambian common mole-rat of the karyotype $2n = 68$ is more closely related to the giant mole-rat than to the common mole-rat of the karyotype $2n = 58$. There is a clear dichotomy between the three Zambian taxa and *C. damarensis*, on the one hand, and *C. h. hottentotus* and *C. h. natalensis*, on the other hand. The relationship (based upon the allozymic variation) does not correspond to the current geographical and ecological distribution or to morphological (particularly coloration and size) differentiation.

Introduction

The family Bathyergidae includes five genera of subterranean hystricognathous rodents endemic to Africa. While four genera are represented by only a single or two species with restricted distribution, one genus – *Cryptomys* – is remarkably polyspecific and occurs from semi-arid to mesic habitats in different soil types over a wide geographical range from Ghana to the Cape Province in South Africa. Extreme variation in many morphological traits makes taxonomic treatment of this genus very difficult. While up to 44 and 49 species of *Cryptomys* have been listed by Allen (1939) and Ellermann (1940), respectively, only three to seven species were recognized by later authors (Nowak and Paradiso 1983 and Honeycutt et al. 1991, respectively). More recently, Filippucci et al. (1994) have examined mole-rats of two populations in Zambia and having identified them as new (formally not yet named) species clearly distinct from those considered by Honeycutt et al. (1991), thus, we have suggested that the number of species of the genus should be higher than seven.

There is a general agreement (for further citations, see Filippucci et al. 1994 and Macholan et al. 1993) that because of extreme morphological variation, systematics of *Cryptomys* has to be based on (or at least should involve) karyology, serology, and molecular genetics. Nevertheless, all students of bathyergid taxonomy also agree that giant mole-rats (*Cryptomys mechowi*) which are morphologically distinct (particularly as far as their body size is concerned) from other *Cryptomys* mole-rats, should be considered a separate species.

Cryptomys mechowi occurs in relatively mesic habitats (annual rainfall over 1,000 mm) in Angola, Zaire, Zambia, Malawi, and Tanzania (e. g., ANSELL and DOWSETT 1988). For a long time, the biology of giant mole-rats has been virtually unknown to zoologists. Only recently we have demonstrated their facultative carnivory and have shown that in contrast to predictions of the "aridity-hypothesis" of eusociality, giant mole-rats are social (BURDA and KAWALIKA 1993). Giant mole-rats have a body weight at least four-times that of the common mole-rats. The white head spot, which is characteristic of the common mole-rats, is completely missing in most individuals of giant mole-rats. Furthermore, we have shown (MACHOLAN et al. 1993) that *C. mechowi* is clearly distinct also in karyotype, having the lowest number of chromosomes (2 n = 40) found among *Cryptomys* so far. It was therefore of interest to examine the taxonomic status of *C. mechowi* also by means of other methods; particularly allozyme analysis which has been employed successfully in the study of the bathyergid taxonomy previously (NEVO et al. 1987; JANECEK et al. 1992; FILIPPUCCI et al. 1994).

Material and methods

Electrophoretic analysis was carried out on four specimens of the giant mole-rat, *Cryptomys mechowi*, collected at the Ndola town periphery (Copperbelt Province, Zambia) and on 18 specimens belonging to two karyotypically distinct forms of common mole-rats, *Cryptomys* sp., from Zambia, characterized by different chromosomal sets: 2 n = 68 (population Lusaka; 15 specimens examined) and 2 n = 58 (population Itezhi-Tezhi – Hot-Springs; 3 specimens). For comparison, samples of *C. h. hottentotus* (6 animals), *C. h. natalensis* (4 animals), and *C. damarensis* (1 specimen) from South Africa, previously analysed and described by NEVO et al. (1987), were used.

Tissues of each specimen were preserved in the laboratory at –80 °C until processed. Homogenates for electrophoresis were obtained from portions of muscle and kidney tissues crushed in distilled water. Genic variation was assessed using standard horizontal starch-gel electrophoresis of enzymes coded for by 31 presumptive loci. All gels were prepared using an 11%-suspension of Connaught hydrolysed starch.

Homogenates obtained from muscle were processed for the following enzymatic proteins: α-glycerophosphate dehydrogenase (E.C. 1.1.1.8; αGpdh), lactate dehydrogenase (E.C. 1.1.1.27; Ldh-1 and Ldh-2), malate dehydrogenase (E.C. 1.1.1.37; Mdh-1 and Mdh-2), malic enzyme (E.C. 1.1.1.40; Me-1 and Me-2), isocitrate dehydrogenase (E.C. 1.1.1.42; Idh-1 and Idh-2), 6-phosphogluconate dehydrogenase (E.C. 1.1.1.44; 6-Pgdh), glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49; G-6-pdh), indophenol oxidase (E.C. 1.15.1.1; Ipo-1 and Ipo-2), nucleoside phosphorylase (E.C. 2.4.2.1; Np), glutamate-oxalacetate transaminase (E.C. 2.6.2.1; Got-1 and Got-2), creatine kinase (E.C. 2.7.3.2; Ck), adenylate kinase (E.C. 2.7.4.3; Adk), phosphoglucomutase (E.C. 2.5.7.1; Pgm-1 and Pgm-2), esterases (E.C. 3.1.1.1; Est-1,Est-2 and Est-3), acid phosphatase (E.C. 3.1.3.2; Acph), aminopeptidase (E.C. 3.4.11; Ap-2), adenosine deaminase (E.C. 3.5.4.4; Ada), fumarase (E.C. 4.2.1.2; Fum), and phosphoglucose isomerase (E.C. 5.3.1.9; Pgi).

Homogenates obtained from kidney were processed for: alcohol dehydrogenase (E.C. 1.1.1.1; Adh), sorbitol dehydrogenase (E.C. 1.1.1.14; Sdh), and xanthine dehydrogenase (E.C. 1.2.3.2; Xdh).

The employed procedures were described by NEVO et al. (1987) and FILIPPUCCI et al. (1988). Isozymes were numbered in order of decreasing mobility from the most anodal one. Allozymes were designated numerically according to their mobility, relative to the most common allele (=100; <100 = slower mobility; >100 = faster mobility) in *C. h. hottentotus* from South Africa.

Allozyme data were analysed with the BIOSYS-1 program of SWOFFORD and SELANDER (1981). Intrapopulational genetic variation was estimated by the following genetic indices: the mean observed (Ho) and expected (He) heterozygosity per locus, the proportion of polymorphic loci in the population under the 1% criterion (i. e., a locus is considered polymorphic if the frequency of the most commmon allele does not exceed 0.99), and the mean number of alleles per locus (A). The amount of genetic divergence between populations was estimated with both NEI's standard and unbiased indices of genetic identity I, and distance D (NEI 1972, 1978). A dendrogram of the genetic relationships among populations was obtained using the UPGMA clustering method (SOKAL and SNEATH 1963).

Results and discussion

Pattern of variation

Fifteen out of the thirty-one loci scored were monomorphic and fixed for the same allele in the three Zambian *Cryptomys* taxa (i. e. Lusaka, Itezhi-Tezhi, and *C. mechowi*). These were in turn: Adh, Sdh, Ldh-1, Ldh-2, Mdh-2, Me-2, Idh-1, Idh-2, Ipo-1, Ipo-2, Got-2, Adk, Pgm-2, Ap-2, Est-2. The allele frequencies of the polymorphic and/or diagnostic loci in the three Zambian *Cryptomys* populations under study are given in table 1. For detailed allele frequencies in South African populations see, Filippucci et al. (1994).

The population from Lusaka, characterized by 2 n = 68, displayed polymorphism at the following loci: αGpdh, Me-1, G6pdh, Got-1, Pgm-1, Ada, Pgi, Acph, Xdh, and Est-3. The Itezhi-Tezhi population, characterized by 2 n = 58, was polymorphic at the following loci: αGpdh, Mdh-1, Me-1, 6Pgdh, Pgi, Pgm-l, and Est-1. Finally, *C. mechowi* was polymorphic at Mdh-1, Np, Got-1, Ck, Pgm-1, and Fum.

Genetic summary

The mean value of expected and observed heterozygosity, proportion of polymorphic loci, and the mean number of alleles per locus are shown in table 2. In the Lusaka sample, the observed heterozygosity (Ho) corroborated well with the value expected under the Hardy-Weinberg equilibrium (He). The obvious discrepancy between He and Ho in the Itezhi-Tezhi population was most probably caused by a bias due to small sample size (cf., also He and Ho in *C. mechowi*). Yet, according to Gorman and Renzi (1979), the effect of a small sample size upon the heterozygosity should be less than 2.5% as compared with a larger sample size.

The overall mean proportion of polymorphic loci (P1%) for the three populations ranged from 0.193 in *C. mechowi* to 0.323 in the Lusaka population. Instead, values of the number of alleles per locus (A) were similar in all three samples (1.193 in *C. mechowi* to 1.323 in Lusaka mole-rats).

The observed genetic variation thus corresponded to the values already observed by Nevo et al. (1987) in South African species of *Cryptomys* and was within the range reported for other rodents in general (Nevo et al. 1990).

Genetic differentiation

Two loci (6Pgdh and Acph) were found discriminant between Lusaka and Itezhi-Tezhi, displaying fixation of alternative alleles, and five loci (αGpdh, Mdh-1, Got-1, Pgi, and Est-1) partially discriminated the two populations. Furthermore, two loci were fixed for alternative alleles in the Lusaka sample and *C. mechowi* (6Phdh and Est-1) and two loci discriminated the latter species and 2 n = 58 species from Itezhi-Tezhi (Acph and Est-1), another two loci (6Pgdh and Pgi) being discriminant partially. In addition, appreciable differences in allelic frequencies were revealed in Pgm-1 between *C. mechowi* and both Zambian populations of common mole-rats.

Genetic distance

For comparison with the South African taxa, *C. h. hottentotus, C. h. natalensis* and *C. damarensis*, the number of loci considered had to be decreased to 22. The following loci were therefore excluded from the subsequent analysis: Sdh, Me-2, Ipo-l, Ipo-2, Ck, Adk, Ap-2, Fum, and Est-3. Since only one specimen of *C. damarensis* was included in

Table 1. Allelic frequencies observed at the polymorphic and/or discriminant loci for the analysed Zambian populations of the genus *Cryptomys*. Number of examined specimens in parentheses

Loci	Alleles	Lusaka	Itezhi-Tezhi	*C. mechowi*
αGpdh		(14)	(3)	(4)
	100	–	–	–
	106	0.93	0.50	1.00
	110	0.07	0.50	–
Mdh-1		(15)	(3)	(4)
	100	1.00	0.67	0.75
	103	–	–	0.25
	105	–	0.33	–
Me-1		(15)	(3)	(4)
	110	0.97	0.67	1.00
	113	0.03	0.33	–
6Pgdh		(15)	(3)	(4)
	100	–	0.83	–
	105	1.00	–	–
	95	–	0.17	1.00
G6pdh		(15)	(3)	(4)
	100	0.23	–	–
	95	0.77	1.00	1.00
Xdh		(13)	(3)	(4)
	100	0.89	1.00	1.00
	105	0.12	–	–
Np		(15)	(3)	(4)
	100	1.00	1.00	0.75
	95	–	–	0.25
Got-1		(15)	(3)	(4)
	100	0.30	–	0.75
	90	0.70	–	–
	105	–	1.00	0.25
Ck		(15)	(3)	(4)
	100	1.00	1.00	0.75
	105	–	–	0.25
Pqm-1		(9)	(3)	(4)
	100	0.94	0.67	–
	103	0.06	0.33	0.50
	105	–	–	0.50
Ada		(13)	(2)	(4)
	105	0.96	1.00	1.00
	109	0.04	–	–
Fum		(15)	(3)	(4)
	100	1.00	1.00	0.88
	95	–	–	0.12
Pgi		(15)	(3)	(4)
	100	0.90	0.17	1.00
	90	–	0.83	–
	96	0.10	–	–
Acph		(11)	(2)	(1)
	100	0.05	–	–
	105	0.95	–	1.00
	110	–	1.00	–
Est-1		(13)	(3)	(4)
	105	1.00	0.50	–
	108	–	0.50	–
	110	–	–	1.00
Est-3		(5)	(2)	(2)
	100	0.90	1.00	1.00
	105	0.10	–	–

Table 2. Values of expected (He) and observed (Ho) heterozygosity, percentage of polymorphic loci (P1%), and average number of alleles per locus (A) based on 31 loci

Population	N	He	Ho	P1%	A
Lusaka	15	0.058	0.057	0.323	1.323
Itezhi-Tezhi	3	0.093	0.043	0.226	1.226
C. mechowi	4	0.071	0.056	0.193	1.193

the analysis, the "biased" Nei's identity and distance indices (Nei 1972) had to be used. A UPGMA dendrogram summarizing the genetic relationships between the populations studied is given in figure 1. (Since the phenogram of the three Zambian taxa based on 31 loci conforms to the corresponding part of the tree constructed for all six taxa, only one figure is presented).

Strikingly, in spite of its conspicuous size differentiation from other *Cryptomys* species, *C. mechowi* revealed the closest relationship to 2n = 68 population of the common mole-rat from Lusaka (D = 0.116). On the other hand, the 2n = 58 species from Itezhi-Tezhi appears to be more distinctly related to both former taxa (D = 0139 and 0.163 respectively).

As already shown by Filippucci et al. (1994) for Lusaka and Itezhi-Tezhi common mole-rats, and now demonstrated also for *C. mechowi*, all three Zambian taxa group together with South African *C. damarensis*, both subspecies of *C. hottentotus* being genetically much more distinct from all other species under study. A clear separation of *C. damarensis* from *C. hottentotus* was demonstrated already in previous studies (Nevo et al. 1987; Janecek et al. 1992; Filippucci et al. 1994). Interestingly, the grouping based upon the genetic distances is reflected also in the numbers of arms of autosomes (cf., Fig. 1). It would be, however, preliminary to speculate at this point about the chromosome speciation in mole-rats. On the other hand, the systematic relationship between Zambian mole-rats and *C. damarensis* does not correspond to the actual

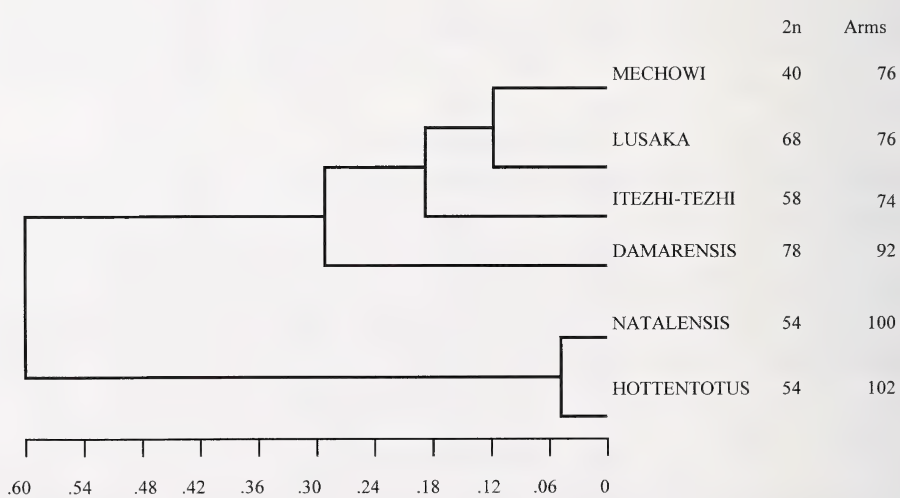


Fig. 1. UPGMA dendrogram summarizing the genetic relationship among populations of the genus *Cryptomys* from Zambia and South Africa. (Data on the number of chromosomes and arms of autosomes are taken from Macholan et al. (1993) and the literature cited therein.)

geographical and ecological distribution. The South African species (*C. h. hottentotus, C. h. natalensis* and *C. damarensis*) occur in dry regions (annual rainfall = 200–600 mm), while Zambian mole-rats originate from rather mesic areas (annual rainfall = 800–1,200 mm).

Zusammenfassung

Allozymdifferenzierung und systematische Beziehungen von sambischen Riesengraumullen, Cryptomys mechowi (Bathyergidae, Rodentia)

Allozymvariation (31 Genloci) wurde bei Riesengraumullen (*Cryptomys mechowi*) und zwei Taxa von Kleingraumullen aus Sambia untersucht. Zum Vergleich wurden parallel Allozyme (22 Genloci) bei *Cryptomys damarensis, C. h. hottentotus* und *C. h. natalensis* aus Südafrika neu analysiert. Der Kleingraumull mit dem Karyotyp 2 n = 68 zeigt eine nähere Verwandtschaftsbeziehung zum Riesengraumull als zum Kleingraumull mit dem Karyotyp 2 n = 58. Es besteht eine klare Dichotomie zwischen den drei untersuchten sambischen Taxa und *C. damarensis* einerseits und *C. h. hottentotus* und *C. h. natalensis* anderseits. Die jetzige geographische und ökologische Verbreitung und die morphologischen (insbesondere Größen- und Fellfarb-)Unterschiede der untersuchten Arten stimmen nicht mit den auf der Allozymvariation beruhenden Verwandtschaftsbeziehungen überein.

References

Allen, G. M. (1939): A checklist of African mammals. Harvard Coll., Cambridge, Mass. USA: Bull. Mus. Comp. Zool.

Ansell, W. F. H.; Dowsett, R. J. (1988): Mammals of Malawi. An annotated check list and atlas. Cornwall: Trendrine Press.

Burda, H.; Kawalika, M. (1993): Evolution of eusociality in the Bathyergidae. The case of the giant mole rats (*Cryptomys mechowi*). Naturwissenschaften **80**, 235–237.

Ellermann, J. R. (1940): The families and genera of living rodents. London: Trustees of the Brit. Mus. Nat. Hist.

Filippucci, M. G.; Burda, H.; Nevo, E.; Kocka (1994): Allozyme divergence and systematics of common mole-rats (*Cryptomys*, Bathyergidae, Rodentia) from Zambia. Z. Säugetierkunde **59**, 42–51.

Filippucci, M. G.; Rodino, E.; Nevo, E.; Capanna, E. (1988): Evolutionary genetics and systematics of the garden dormouse, *Eliomys* Wagner, 1840. 2-Allozyme diversity and differentiation of chromosomal races. Boll. Zool. **55**, 47–54.

Gorman, G. C.; Renzi, J. Jr. (1979): Genetic distance and heterozygosity estimates in electrophoretic studies. Effects of sample size. Copeia 1979, 24–249.

Honeycutt, R. L.; Allard, M. W.; Edwards, S. V.; Schlitter, D. A. (1991): Systematics and evolution of the family Bathyergidae. In: The Biology of the Naked Mole-Rat. Ed. by P. W. Sherman, J. U. M. Jarvis, and R. D. Alexander. Princeton, New Jersey: Princeton Univ. Press. Pp. 66–96.

Janecek, L. L.; Honeycutt, R. L.; Rautenbach, I. L.; Erasmus, B. H.; Reig, S.; Schlitter, D. A. (1992): Allozyme variation and systematics of African mole-rats (Rodentia: Bathyergidae). Biochem. Syst. Ecol. **20**, 401–416.

Macholan, M.; Burda, H.; Zima, J.; Misek, I.; Kawalika, M. (1993): Karyotype of the giant mole-rat, *Cryptomys mechowi* (Rodentia, Bathyergidae). Cytogenet. Cell Genet. **64**, 261–263.

Nei, M. (1972): Genetic distance between populations. Am. Nat. **106**, 283–292.

Nei, M. (1978): Molecular Evolutionary Genetics. New York: Columbia Univ. Press.

Nevo, E.; Ben-Shlomo, R.; Beiles, A.; Jarvis, J. U. M.; Hickman, G. C. (1987): Allozyme differentiation and systematics of the endemic subterranean mole rats of South Africa. Biochem. Syst. Ecol. **15**, 489–502.

Nevo, E.; Filippucci, M. G.; Beiles, A. (1990): Genetic diversity and ist ecological correlates in nature: Comparison between subterranean, fossorial and aboveground small mammals. In: Evolution of Subterranean Mammals at the Organismal and Molecular Levels. Ed. by E. Nevo and A. O. Reig. New York: Allan R. Liss. Pp. 347–366.

Nowak, R. M.; Paradiso, J. L. (1983): Walker's Mammals of the World. 4th ed. Baltimore, London: The John Hopkins Univ. Press.

Sokal, R. R.; Sneath, P. N. A. (1963): Principles of Numerical Taxonomy. San Francisco: W. H. Freeman.

Swofford, D. L.; Selander, R. B. (1981): BIOSYS-1: A Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics. J. Hered. **72**, 281–283.

Authors' addresses: Maria G. Filippucci, Department of Biology, University of Roma "Tor Vergata", Via E. Carnevale, I-00173 Roma, Italy; Mathias Kawalika, P. O. Box 7 37 96, Ndola, Zambia; Milos Macholan, Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, Veveri 97, CZ-60200 Brno 2, Czech Republic; Andreas Scharff and Hynek Burda*, Department of General Zoology, Faculty of Biology, University of Essen, D-45117 Essen, Germany (* from whom the reprints should be requested).

Z. Säugetierkunde **62** (1997) 179–181

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Distribution and range expansion of Savi's bat (*Hypsugo savii*) in Austria

By FRIEDERIKE SPITZENBERGER

Natural History Museum in Vienna, Vienna, Austria

Receipt of Ms. 18. 11. 1996
Acceptance of Ms. 22. 01. 1997

The German name „Alpenfledermaus" (alpine bat) goes back to BLASIUS (1857), who recorded this species between 1847 and 1852 from several sites in the Alps between Montblanc in the Swiss western Alps and Salzburg in the Austrian eastern Alps. This bat used to live in huts in high altitudes above the tree line. BLASIUS (1857) did not mention this species at lower elevations. 100 years later KAHMANN (1958) found a group of *Hypsugo savii* in a loft of a house in the small town of Mittenwald situated in the Bavarian Alps north of the main chain in 912 m altitude. While nowadays in Switzerland *Hypsugo savii* is found to be common in alpine valleys south of the Alps as well as in valleys climatically influenced by "föhn"-winds north of the Alps (ARLETTAZ and ZINGG 1995), KAHMANN'S (1958) record is the last evidence of a high altitude population of *H.savii in the eastern Alps.*

The alpine population of *H. savii*, described by BLASIUS (1857) to be rather common at high altitudes, was reported in 1988 by SPITZENBERGER and MAYER to be scarce or missing in Austria. The only recent Austrian record at that time was the finding of a female in a factory building in the town of Klagenfurt in January 1985. Klagenfurt, the capital of Carinthia, lies south of the main chain of the Alps at an altitude of ±450 m above sea level. This winter record later proved to be the first sign of a resident population in Klagenfurt: On 18 July 1993 a single dead female and her offspring and in January 1994 another hibernating specimen were found in buildings in Klagenfurt (SPITZENBERGER 1995).

While there were still no new observations of this species in the Austrian Alps, in the following two years Savi's bat was recorded three times northeast of Klagenfurt at lower elevations: Probably 1995 (no exact date mentioned): one dead specimen in the castle of Klaffenau near Hartberg, Styria, 330 m above sea level. (FREITAG 1996).

16. Feb. 1995: one female in Vienna (9th district), 166 m above sea level.

25. Sept. 1996: one male in Vienna (9th district).

Dates and localisations in records of Savi's bat in Austria between 1994 and 1996 (Fig. 1) appear to indicate a short-termed expansion of this species northeastward, using a route around the southeastern margins of the Alps. From Klagenfurt in the Carinthian basin the species spread 150 km to the northeast (Hartberg) and appeared 110 km further north-northeast in Vienna in 1995. At the same time Kuhl's pipistrelle, a predominantly Mediterranean species, occurring also in semi-deserts of the Near East, spread in Austria to the northeast, apparently using the same route as *H. savii* (BAUER 1996). These two species of bats live together on the Adriatic islands (see for instance GAISLER 1994) and specimens of both species have been found as far from their normal ranges as England in recent times (GANTLETT 1993; FISHER 1996).

Fig.1. Historical (empty circles) and recent (full circles) distribution of Savi's bat (*Pipistrellus savii*) in Austria.

Hypsugo savii is a petrophilous paleo-xeromontane faunal element. In Middle Asia it is a typical bat of rocky mountainous areas (Strelkov 1980). Rybin et al. (1978) presumed *H. savii* to be present in all rocky regions of southern Kirghizia. They found a small colony at an altitude of 3 100 m above sea level. However in Kazakhstan it also inhabits lower elevations, where it occurs in huts of sheperds (Strelkov and Shaimardanov 1983). In Turkmenia it was also found in a large modern town (Ashkhabad) (Strelkov et al. 1978). This adaptability to human habitats may have faciliated its expansion to the lowlands such as in the black redstart (Burton 1995). This bird, originally confined to dry and warm rocky slopes of high mountains, began to spread to the plains of Germany and north into Denmark as well as to southern England in the middle of the last century (Burton 1995). Knopfli (1971) believes, that the bird's ability to use human buildings instead of crevices in rocks was the main reason for its success in expanding into the lowlands and thereby extending its range.

In the southern parts of its European distribution *H. savii* ranges regularly from high to low altitudes. In Iberia it was found between 2 400 m and 150 m above sea level (Ibanez et al. 1992); in the French-Swiss border region it occurs from 1 900 m (Col du Bretolet, Valais – Arlettaz and Zingg 1995) to 200 m altitude (Saint Fons, S of Lyon in the Lower Rhone valley – Ariagno 1993). In the Swiss Bregaglia Valley (GR) it is distributed from 1 810 m to 320 m above sea level (Zingg and Maurizio 1991) and on the Balkan Peninsula from 1 350 m (Kozuv mountains – Martino 1939 fide Kryštufek et al.1992) to sea level (several Adriatic islands – Petrović 1983).

As Austria's bat fauna is quite well studied, it can be ruled out that *H. savii* occurs here regularly from the low altitudes, where it has been found recently, to high mountain regions. It can be assumed, that the ancestral Alpine population that occurred in the eastern Alps during a climatically favourable period 150 years ago, has since become extinct. The recently expanding population is obviously an urban one and adapted to lower altitudes. Its origin may be looked for in northern Italy, where *H. savii* it is one of the most common inhabitants of towns (Padova, Treviso, Venezia, Verona – Vernier 1996).

References

ARIAGNO, D. (1993): Une 19^{e} espèce de Chroptère pur le departement du Rhone: le Vespère de Savi (*Ypsugo savii*). Le Bièvre **13**, 118.

ARLETTAZ, R.; ZINGG, P, (1995): *Hypsugo savii* (Bonaparte, 1837). In: Säugetiere der Schweiz. Ed. by J. HAUSSER. Basel, Boston, Berlin: Birkhäuser. Pp. 162–166.

BAUER, K. (1996): Ausbreitung der Weißrandfledermaus *Pipistrellus kuhlii* (Kuhl, 1819) in Österreich. Mitt. Abt. Zool. Landesmus. Joanneum **50**, 17–24.

BLASIUS, J. (1857): Fauna der Wirbelthiere Deutschlands. 1. Bd. Säugetiere. Braunschweig: Viehweg.

BURTON, J. F. (1995): Birds and climate change. London: Christopher Helm.

FISHER, C. (1996): Savi's Pipistrelle *Pipistrellus savii* in Britain. Abstracts VIIth European Bat Res. Symp. Veldhoven. Pp. 18–19.

FREITAG, B. (1996): *Pipistrellus savii* (Bonparte, 1837) – Erstnachweis für die Steiermark (Mammalia, Chiroptera). Mitt.naturwiss. Ver.Steiermark **125**, 237–238.

GAISLER, J. (1994): The bats *Pipistrellus kuhli* and *Hypsugo savii* on the Island of Rab (Croatia). Folia zool. **43**, 279–280.

GANTLETT, S. (1993): Another mammal new to Britain. Birding World **6**, 88.

IBANEZ, C.; GUILLEN, A.; FERNANDEZ, R.; PEREZ, J. L.; GUERRO, S. I. (1992): Iberian distribution of some little known bat species. Mammalia **56**, 433–444.

KAHMANN, H. (1958): Die Alpenfledermaus *Pipistrellus savii* Bonaparte, 1837 in den Bayerischen Alpen, und biometrische Mitteilungen über die Art. Zool. Anz. **160**, 87–94.

KNOPFLI, W. (1971): Die Vogelwelt der Limmattal- und Zürichseeregion. Ornithol. Beobachter **68**, Beiheft, 1–174.

KRYŠTUFEK, B.; VOHRALÍK, V.; FLOUSEK, J.; PETROVSKI, S. (1992): Bats (Mammalia: Chiroptera) of Macedonia, Yugoslavia. In: Prague Studies in Mammalogy. Ed. by I. HORÁČEK and V. VOHRALÍK. Praha: Karolinum-Charles Univ. Press. Pp. 93–111.

MARTINO, V. (1939): Materijali po ekologii zoogeografii Juznoi Serbiji. Zap. Russ. nauc. inst. Bjelgrad **14**, 85–106.

PETROVIĆ, P. (1983): A new mammal species in the fauna of the Socialist Republic of Serbia: the Savi's Pipistrelle, *Pipistrellus savii* Bonaparte, 1837, (Chiroptera, Mammalia). Proc. Faun. SR Serbia **2**, 263–266.

RYBIN, S.; HORÁCEK, I.; ČERVENÝ, J. (1987): Bats of southern Kirghizia: Distribution and faunal status. In: Europ.Bat Research. Ed. by V. HANÁK, I. HORÁČEK, and J. ČERVENÝ. Praha: Charles Univ. Press. Pp. 421–441.

SPITZENBERGER, F. (1995): Die Säugetiere Kärntens Teil 1. Carinthia II **185/105**, 247–352.

SPITZENBERGER, F.; MAYER, A. (1988): Aktueller Stand der Kenntnis der Fledermausfauna Osttirols und Kärntens; zugleich Mammalia austriaca 14 (*Myotis capaccinii* Bonaparte, 1837), *Pipistrellus kuhli* Kuhl, 1819 und *Pipistrellus savii* Bonaparte, 1837. Ann. Naturhist. Mus. Wien **90 B**, 69–91.

STRELKOV, P. P. (1980): The bats (Chiroptera, Vespertilionidae) of Central and West Kasakhstan. Sistematika, biologia i morfologia mlekopitayushchikh fauni SSSR. Tr. zool. inst. Ak. nauk SSSR Leningrad **99**, 99–123 (in Russ.).

STRELKOV, P. P.; SHAIMARDANOV, R. T. (1983): The new data on the distribution of bats (Chiroptera) in Kazakhstan. Fauna, sistematika i biologia mlekopitayushchikh. Tr. zool. inst. Ak. nauk SSSR Leningrad **119**, 3–42 (in Russ.).

STRELKOV, P. P.; SOSNOVTZEVA, V. B.; BABAEV, H. B. (1978): The bats of Turkmenia. Funkzionalnaja morfologia i sistematika mlekopitayushchikh. Tr. zool. inst. Ak. nauk SSSR Leningrad **79**, 3–71 (in Russ.).

VERNIER, E. (1996): *Hypsugo savii* (Bonparte, 1837) – Pipistrello di Savi. In: Atlante dei Mammiferi del Veneto. Ed. by M. BON, P. PAOLUCCI, F. MEZZAVILLA, R. DE BATTISTI, and E. VERNIER: Lavori Soc. Ven. Sci. Nat., suppl. **22**, 50.

ZINGG, P.; MAURIZIO, R. (1991): Die Fledermäuse (Mammalia: Chiroptera) des Val Bregaglia/GR. Jber. Natf. Ges. Graubünden **106**, 43–88.

Author's address: Dr. FRIEDERIKE SPITZENBERGER, Naturhistorisches Museum, Postfach 417, A-1014 Wien

Z. Säugetierkunde 62 (1997) 182–186

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

On extralimital records of Hooded seals, *Cystophora cristata* (Erxleben, 1777), on the western European continental coast

By P. J. H. van Bree

Zoölogisch Museum, Universiteit van Amsterdam, Amsterdam, the Netherlands

Receipt of Ms. 17. 06. 1996
Acceptance of Ms. 26. 10. 1996

In a detailed article on the hooded seal, *Cystophora cristata*, Mohr (1963) also devoted a chapter to records of stragglers of this arctic species along European coasts. She listed nine animals found along the coast of Norway, six on the coasts of the United Kingdom, and only one from the continental coast of western Europe (northern Denmark to southern Spain). The latter concerned a young male, with a length of 125 cm, caught between Oleron Island and continental France, in July 1843 (see e. g. Robineau 1992). This specimen was to become the holotype of *Phoca isidorei* Lesson, 1843, a junior synonym of *Cystophora cristata.* Today, more than 30 years since publication of Mohr's (1963) article, at least 33 more specimens have become known from western European continental coasts (Tab. 1). In the present study not only the extralimital records are listed but also additional data on some of these records are presented. The numbering of records refers to the listing in table 1.

Animals 5 and 6, both from the Netherlands, most probably passed the floodgate which was constructed in the Oosterschelde, Province of Zeeland, in 1986. Animal 5 was transferred to the Seal Rescue Centre at Pieterburen, and, after recovery, it was marked and released in the North Sea. It returned, however, to the Netherlands' coast and was observed at the Engelsmanplaat, a high-lying shoal in the Wadden Sea. Some time later, it was caught again at the Leybucht in western Niedersachsen, Germany. It was set free again at Skagen in northern Denmark and was not observed thereafter. The animals 12 and 13 entered rivers and were found far from sea. The last one, found in the river Scheldt near the French-Belgium border, swam at least 640 km, if we take the town of Vlissingen (Flushing) as starting point of the trip. In this rather polluted river it passed thereby a number of locks; quite some performance!

In addition, an old extralimital record of hooded seal, which has not been mentioned in the zoological literature so far, may be rescued from obscurity here. This concerns a pregnant female, which was killed at the river Merwede, between Gorkum and Werkendam, Province of Zuid-Holland, the Netherlands, on 10 March 1600, and depicted in a plate by Julius Goltzius (Fig. 1). Identification is based on length (said to be nine feet, but prudently estimated as more than 2 m), weight (ca. 226 kg), and the spotted coat. Moreover, the seal carried a full-grown fetus. In grey seals, *Halichoerus grypus*, the pupping season is much earlier, while in common seals, *Phoca vitulina*, in the Netherlands, the reproduction season is from late June to early August. The state of pregnancy of the animal from 1 600 fits well with the known reproduction period of hooded seals. Seal 7 (Tab. 1) represents another pregnant specimen encountered on West-European coasts (see Ibáñez et al. 1988). There is also a record of a hooded seal giving birth on the coast of Norway, 7 April 1980 (Øritsland and Bondø 1980).

Table 1. List of extralimital records of hooded seals, *Cystophora cristata*, on the western European continental coast.

Nr	Sex	Locality	Départment/ Province/Land	Country	Date	Length (cm)	Weight (kg)	References
1	♀	Bidassoa, nr. Hendaye	Pyrénées-Atlantique	F	13. VII. 1978	164		Duguy (1979): Pouvreau et al. (1980)
2	♀	Island of Fanø	Ribe	DK	24. VIII. 1978	118	38	Wolff (1981): Tougaard (1987)
3	♂	Praia Verde, Monte Gordo	Algarve	P	24. VI. 1979	104	27	Reiner (1979
4	♂	Praia del Norte	Peniche	P	2. VI. 1980	150	94	Reiner (1980): Teixeira (1980)
5	♂	Kreekrak locks, nr. Rilland/Bath	Zeeland	NL	30. VII. 1981	175	±200	Wolff (1981): Borkenhagen (1994)
6	♀	Oosterschelde, nr. Ourwerkerk	Zeeland	NL	9. VI. 1982		29.2	't Hart in litt. (1990)
7	♀	Torre Zalabar 36°54′N, 6°24′W	Huelva	E	26. II. 1983	201	116	Ibañez et al. (1988)
8	♀	Playa de São Torpes (Sines)	Setúbal	P	17. VII. 1983	129		Ignacio and De Melo (1987)
9	♂	Jadebusen nr. Wilhelmshaven	Niedersachsen	D	21. VIII. 1984		40	Schumann (1986)
10	♂	Hemmes de Marck nr. Calais	Pas-de-Calais	F	3. IX. 1985	111	36	Duguy (1986)
11	♂	Sta. María de Oia	Pontevedra	E	V. 1986	100	25	Valeiras Mata (1995)
12	♀	Royan	Charente-Maritime	F	20. VII. 1986	139	73.5	Duguy (1987)
13	♀	Castet-en-Dorthe nr. Langon	Gironde	F	13. VIII. 1986	102	27	Duguy (1987)
14	♀	Kain-lez-Tournai locks nr. Tournai/Doornik	Hainaut	B	12. III. 1987	160	±120	't Hart in litt. (1987)
15	♂	off Comillas 43°22′4″N,4°17′W	Santander	E	24. V. 1987	159		García Castrillo et al. (1988)
16	♀	Rocher des Charpentiers nr. Saint Nazaire	Loire-Atlantique	F	19. VII. 1988	105	26	Duguy (1989)
17	♂	N of Cadzand	Zeeland	NL	20.X. 1988		120	't Hart in litt. (1988)
18	♀	Puerto de Huelva	Huelva	E	9. VI. 1990	94	19	Van der Kamp in litt. (1991): Cebrián in Avella et al. (1993)
19	♀	Playa de las Lances nr. Tarifa	Cádiz	E	3. VII. 1990	105	21	Van der Kamp in litt. (1991): Cebrián in Avella et al. (1993)
20	♂	Norden	Niedersachsen	D	29. VIII. 1990	130	39	Schumann in litt. (1994)
21	♂	Isalnd of Vlieland	Friesland	NL	5. IX. 1990		43	't Hart in litt. (1990)
22	♂	Sables d'Olonne	Vendée	F	6. VII. 1992	±160	110	Duguy in litt. (1992)
23	♀	Gravelines	Pas-de-Calais	F	20. IX. 1992	129	48	Duguy in litt. (1992): 't Hart in litt. (1992)
24	♀	Island of Amrum	Schleswig-Holstein	D	18. VIII. 1993	115	29	Borkenhagen (1994): Heidemann in litt. (1994)
25	♀	Island of Langeoog	Niedersachsen	D	21. IX. 1994		36.5	Schumann in litt. (1994)
26	♀	Dagebüll – Hafen	Schleswig-Holstein	D	29. VII. 1995	114	33	Wollny-Goercke in verbis (1996)

Table 1. (Continued)

Nr	Sex	Locality	Département/ Province/Land	Country	Date	Length (cm)	Weight (kg)	References
27	♂	Jadebusen (Dangast)	Niedersachsen	D	5. X. 1995	95	30	Schumann (1996)
28	♂	Island of Texel (Oudeschild)	Noord-Holland	NL	31. VIII. 1996		36	Brugge in verbis (1996)
29	♀	Boulogne-sur-Mer	Nord	F	5. IX. 1996	103	34	't Hart in verbis (1996)
30	♀	Dike near Ferwerd	Friesland	NL	14. IX. 1996	112	31	Vedder in verbis (1996)
31	♀	Scheveningen harbour	Zuid-Holland	NL	29. IX. 1996	107	34	't Hart in verbis (1996)
32	♂	Wilhelmshafen	Niedersachsen	D	30. IX. 1996	106	40	Rabenstein in verbis (1996)
33	♀	Island of Vlieland (de Hors)	Friesland	NL	5. X. 1996	106	38.5	Vedder in verbis (1996)
34	♂	Island of Baltrum (Ostende)	Niedersachsen	D	8. X. 1996	95	34	Rabenstein in verbis (1996)

Looking at the weights and lengths of the animals in table 1, it becomes clear that the majority of hooded seals encountered along the continental West-European coasts are animals of less than one year of age. Some apparently refer to animals 1–2 years old (13, 16, 21), while two others were subadults or adults (5, 7).

At birth, hooded seals have a length of about 105 cm and a weight of ca. 20 kg. Within the very short lactation period of only four days, they gain more than 5 kg weight per day. They shed their first coat (lanuga) intra-uterine and thus are born with their immature coat, which is blue-grey on the back and silvery-grey laterally and ventrally. It is for this pelt, that "blue-backs" were and are killed in great numbers. They loose this immature coat at an age of about 14 to 15 months. Most of the hooded seals found on European coasts still have this coat. These animals are rather easy to recognize by their relatively large size, their rather broad heads, and their silvery-blue pelts.

After their moult they become light-grey with irregular brown-black spots and blotches; the front of their heads and their fore-flippers are almost black. They keep this type of coat their whole lives. Adult males can inflate in a spectacular way the dorsal part of their noses (the hoods) and also a red bladder (the red very elastic nasal septum), can be forced out of one nostril. The chance, however, that we will see the inflated hood and the red nose bladder on West-European coasts is rather small as till now no full-grown males have been encountered.

Adult females can reach a length of 200 cm and a weight of between 140 to 300 kg; males a length of 260 cm and a weight of between 190 to 350 kg. Skulls of adult specimens can easily be identified. Compared to the length of the skull, they are very broad and the facial part of the skull is rather small as compared to the length of the braincase (see Duguy and Robineau 1992). Skulls of young hooded seals are still more *Phoca*-like but also can be recognized by their width.

Like adults, intact young hooded seals are also rather easily recognized. On one occasion, however, when a young hooded seal was brought in, the author witnessed that three of five naturalists present identified the animal as an aberrant common seal, *Phoca vitulina*, thus demonstrating that it is very conceivable that young hooded seals have been regularly misidentified in the past. This would explain the very small numbers of extralimital records in the past. Presumably, the increase of extralimital

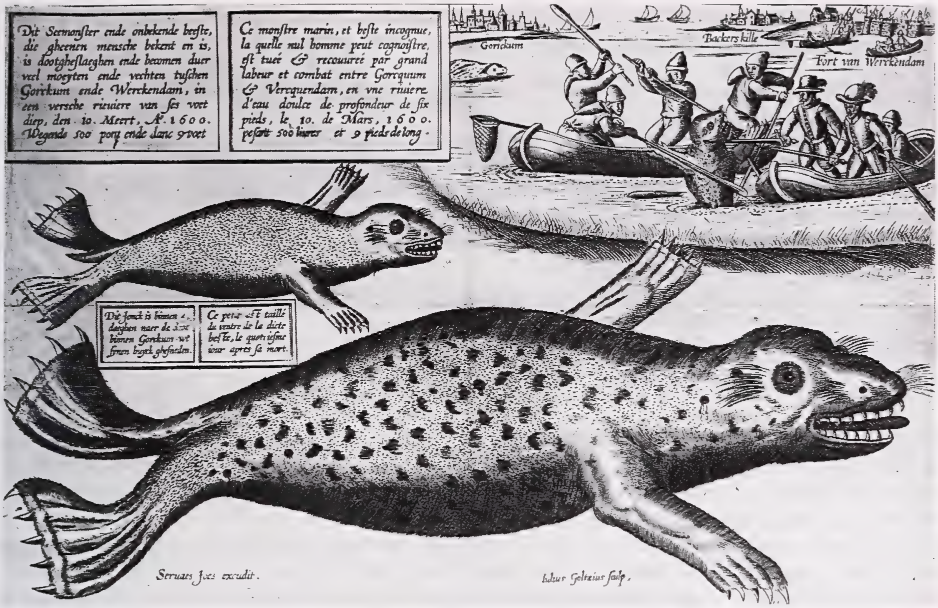


Fig. 1. Print of a pregnant hooded seal and its mature fetus killed in the river Merwede, between Gorkum and Werkendam, the Netherlands, on 10 March 1600. JULIUS GOLTZIUS fecit. Published by courtesy of the Museum van Gijn, Dordrecht.

records during the last decades is for the most part, if not entirely, due to increased observer effort and the availability of better identification manuals rather than to a more frequent occurrence of the species. In addition, the establishment of seal rescue centres has provided the opportunity to observe and study stranded seals at close quarters and to identify them correctly. This situation is comparable to that in ringed seals, *Phoca hispida*, and harp seals, *Phoca groenlandica*, extralimital records of which have also increased significantly in recent years (cf. VAN BREE 1996, VAN BREE et al. 1994).

It is clear, however, that concerning the last animals we have to do with a kind of invasion. In view of the localities where the animals have been found, one gets the impression that the seals did not come from the north along the Scandinavian coast, but directly from the Arctic in a SSE direction. Concerning the cause of the invasion nothing can be said yet.

Acknowledgements

The author is grateful for the data concerning hooded seals he received from Mr H. N. BRUGGE, Dr R. DUGUY, Mrs L. 'T HART, Mr P. 'T HART, Dr G. HEIDEMANN, Drs J. S. VAN DER KAMP, Mr F. RABENSTEIN, Mr W. SCHUMANN, Drs E. J. VEDDER, Mrs K. WOLLNY-GOERKE. He also is thankful for the editorial help he received from Dr W. N. ELLIS and Dr C. J. HAZEVOET. Mrs ALMA KUIPER-RUEMPOL is thanked for drawing the author's attention to the print by J. GOLTZIUS.

References

AVELLÁ, F.; CASTELLS, A.; MAYO, M. (1993): Los pinnípedos de las costas atlánticas y cantábricas de la península Ibérica. Quercus **85**, 29–34.

Borkenhagen, P. (1994): Nachweise nichtheimischer Robbenarten (*Odobenus rosmarus*, *Phoca hispida*, *Phoca groenlandica*, *Cystophora cristata*) an den Küsten Schleswig-Holsteins, Säugetierk Inf. **3**, 661–671.
Bree, P. J. H. van; Vedder, E. J.; 't Hart, L. (1994): Over zadelrobben, *Phoca groenlandica*, op de kust van continentaal West-Europa. Lutra **37**, 97–105.
Bree, P. J. H. van (1996): Extralimital records of the Ringed Seal, *Phoca hispida* Schreber, 1775, on the West-European continental coast. Bonner Zool. Beitr. **46**, 377–383.
Duguy, R. (1979): Rapport annuel sur les Cétacés et Pinnipèdes trouvés sur les côtes de France. Ann. Soc. Sci. nat. Charente-Maritime **6**, 463–474.
Duguy, R. (1980): Rapport annuel sur les Cétacés et Pinnipèdes trouvés sur les côtes de France. Ann. Soc. Sci. nat. Charente-Maritime **6**, 615–632.
Duguy, R. (1986): Rapport annuel sur les Cétacés et Pinnipèdes trouvés sur les côtes de France. Ann. Soc. Sci. nat. Charente-Maritime **7**, 507–522.
Duguy, R. (1987): Rapport annuel sur les Cétacés et Pinnipèdes trouvés sur les côtes de France. Ann. Soc. Sci. nat. Charente-Maritime **7**, 617–639.
Duguy, R. (1988): Les phoques des côtes de France. Ann. Soc. Sc. nat. Charente-Maritime, Suppl. **1988**, 1–52.
Duguy, R. (1989): Rapport annuel sur les Cétacés et Pinnipèdes trouvés sur les côtes de France. Ann. Soc. Sci. nat. Charente-Maritime **7**, 781–808.
Duguy, R.; Robineau, D. (Hrsg.) (1992): Meeressäuger. Teil II: Robben. Handbuch der Säugetiere Europas. Wiesbaden: Aula Verlag.
Garcia-Castrillo, G.; Cendrero, O.; Perez, C.; Nores, C. (1988): Les mammifères marins du Nord de l'Espagne en 1987. Cons. internat. Explor. Mer; C. M. 1988/N: **4**, 1–4.
Ibáñez, C.; Delibes, M.; Castroviejo, J.; Martín, R.; Beltrán, J. F.; Moreno, S. (1988): An unusual record of Hooded Seal (*Cystophora cristata*) in SW Spain. Z. Säugetierkunde **53**, 189–190.
Ignacio, A. M.; Melo, A. de (1987): Portugal-Marine Mammal Committee. Internat. Counc. Explor. Sea; C. M. 1987/N: **1**, 20–22.
Mohr, E. (1963): Beiträge zur Naturgeschichte der Klappmütze, *Cystophora cristata* Erl., 1777. Z. Säugetierkunde **28**, 65–84.
Øritsland, T.; Bondø, G. (1980): Klappmyssunge født på norskekysten. Fauna **33**, 74–76.
Pouvreau, B.; Duguy, R.; Alzieu, Cl; Babin, Ph. (1980): Capture d'un phoque à crête, *Cystophara cristata* (Erxleben, 1777), sur la côte française atlantique et recherches sur sa pathologie. Bull. Centr Etud. Rech. sci. Biarritz **13**, 7–12.
Reiner, F. (1979): Notas sobre a ocurrência de alguns pínipedes na costa portuguesa. Mems. Mus. Mar, Portugal **1**, 1–24.
Reiner, F. (1980): Nota sobre a segunda ocorrência de uma foca de mitra, *Cystophora cristata* (Erxleben, 1777), nas castas de Portugal. Mems Mus. Mar. Portugal **1**, 1–24.
Robineau, D. (1992): Les types de carnivores marins (pinnipèdes) actuels du Muséum national d'Histoire naturelle: Otaridae et Phocidae. Bull. Mus. natl. Hist. nat. Paris, (4) **14** (A), 251–267.
Schumann, W. (1986): Dokumentation, Nr 5, 1986. Seehundaufzucht und Forschungsstation Norden-Norddeich 1–67.
Schumann, W. (1996): Seehunde und Meeressäuger: Dokumentation 1995. Seehundaufzucht und Forschungsstation Norden-Norddeich 1–64.
Teixeira, A. M. (1980): Sobre o aparecimento de dois mammifères marin hos na costa portuguesa – *Cystophora cristata* (Erxleben, 1777) e *Balaenoptera physalus* (Linnaeus, 1758). Rel. Activades do Aquario Vasco da Gama **7**, 1–11.
Tougaard, S. (1987): Første fund af klapmyds (*Cystophora cristata*) i Danmark. Flora og Fauna **93**, 75–76.
Valeiras Mata, X. (1995): Varamento dunha foca de capelo, *Cystophora cristata* (Erxleben, 1777), na Costa de Galicia no 1986. Eubalaena, **7**, 6–11.
Wolf, W. J. (1981): The status of marine mammals in the Wadden Sea area: 7–14. In: Marine mammals of the Wadden Sea. Ed. by P. J. H. Reynders and W. J. Wolf. Leiden, St. Veth tot Steun aan Waddenonderzoek. Pp 7–14.

Author's address: Dr. Peter J. H. van Bree, Zoölogisch Museum, Universiteit van Amsterdam, Mauritskade 61, NL-1092 AD Amsterdam.

Z. Säugetierkunde 62 (1997) 187–190

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Die Tibialänge als Maß für Körpergröße und als Hilfsmittel zur Altersbestimmung bei Siebenschläfern (*Myoxus glis* L.)

Von W. Schlund

Abt. Verhaltensphysiologie, Universität Tübingen, Tübingen Deutschland

Receipt of Ms. 25. 06. 1996
Acceptance Ms. 26. 10. 1996

Bei Freilandarbeiten an lebenden und nicht narkotisierten Siebenschläfern ist eine exakte und vergleichbare Messung der Kopf-Rumpflänge häufig nicht möglich, da die Tiere unterschiedliche Körperhaltungen einnehmen können. Viele Autoren benutzten deshalb im Freiland nur die Masse der Tiere, um so die körperliche Verfassung der Siebenschläfer abschätzen zu können (z. B. v. Vietinghoff-Riesch 1960; Hönel 1991; Bieber 1995). Bei Kleinsäugern und insbesondere bei Winterschläfern unterliegt die Körpermasse jedoch starken jahreszeitlichen Schwankungen und reicht deshalb zur Einschätzung der körperlichen Verfassung alleine nicht aus. Außerdem können auch kleinere Tiere bei ausreichend hohem Körpergewicht eine gute körperliche Konstitution haben. Die Körpermasse der Tiere muß deshalb mit einem geeigneten Maß für Körpergröße in Beziehung gesetzt werden. Bei Vögeln wird dazu häufig die Tarsus-Metatarsuslänge benutzt (z. B. Nur 1984 a, b). In der vorliegenden Arbeit wird untersucht, ob bei Siebenschläfern die Tibialänge ein geeignetes Maß für Körpergröße darstellt.

Auch die Altersbestimmung der Siebenschläfer ist im Freiland nicht immer eindeutig. Es wird deshalb ebenfalls untersucht, ob die Tibialänge eine Alterseinteilung von Siebenschläfern nach Popow (in v. Vietinghoff-Riesch 1960) unterstützt und zur Altersbestimmung juveniler Tiere während der ersten 40 Lebenstage verwendet werden kann. In einer 3jährigen Populationsstudie an Siebenschläfern wurden von 1993 bis 1995 in einem Laubwald (8 ha) und einem Nadel-Laubmischwald (12 ha) bei Tübingen wöchentlich von Mai bis Oktober 80 bzw. 91 Nistkästen auf Belegung durch Siebenschläfer kontrolliert (Schlund 1996; Schlund und Scharfe 1996). In den Nistkästen angetroffene Tiere wurden mit Transpondern individuell markiert (Schlund 1995), gewogen sowie die Kopf-Rumpflänge (KRL), Schwanzlänge (SL), Hinterfußlänge (HFL) und Tibialänge (gemessen einschließlich der Ferse bis Oberkante Knie; TL) bestimmt.

Wie erwartet waren Kopf-Rumpflänge und Hinterfußlänge nur mit großer Ungenauigkeit zu messen. Da Siebenschläfer über die Möglichkeit der Schwanzautotomie verfügen, war aber auch häufig die Schwanzlänge unzuverlässig. Exakt und zuverlässig meßbar war dagegen die Tibialänge. Bei der Überprüfung der Tibialänge als Ersatzmaß für „Körpergröße" ergaben sich außerdem hochsignifikante positive Korrelationen zwischen der Tibialänge und den anderen Körpermaßen (Korrelation nach Pearson: TL vs. KRL: $r = 0{,}45$, $p < 0{,}0001$, $n = 157$; TL vs. HFL: $r = 0{,}33$, $p < 0{,}0001$, $n = 159$; TL vs. SL: $r = 0{,}45$, $p < 0{,}0001$, $n = 147$), die stets höher lagen als die Korrelationen der anderen Maße untereinander (KRL vs. HFL: $r = 0{,}29$, $p < 0{,}0001$, $n = 157$; KRL vs. SL: $r = 0{,}41$, $p < 0{,}0001$, $n = 145$; HFL vs. SL: $r = 0{,}27$, $p < 0{,}0001$, $n = 148$). Die Tibialänge kann demnach bei Siebenschläfern sehr gut als Maß für „Körpergröße" benützt werden. Die körperliche Verfassung der Tiere läßt sich dann über den Quotienten aus Körpermasse und Tibialänge berechnen (Schlund 1996; Schlund und Scharfe 1996).

Nach POPOW (in v. VIETINGHOFF-RIESCH 1960) werden bei Siebenschläfern drei Altersgruppen unterschieden: Juvenil (von der Geburt bis zum ersten Winterschlaf), Subadult (das Jahr nach dem ersten Winterschlaf), Adult (ab dem zweiten Lebensjahr; hier werden die Siebenschläfer in der Regel geschlechtsreif). Da Fellfärbung, Körpergröße, Körpermasse und sexuelle Aktivität nicht immer die Trennung zwischen Subadulten und Adulten ermöglichen, habe ich die Altersbestimmung nach Beendigung der Freilandarbeiten über die Tibialänge der Tiere durchgeführt. Dazu bestimmte ich die 25%- und 75%-Quartile der Tibialängen derjenigen Siebenschläfer, die aufgrund der Individualmarkierung im Jahre 1995 eindeutig als Adult (geboren vor 1993; 1993 reproduzierten die Siebenschläfer nicht, siehe dazu SCHLUND 1996; SCHLUND und SCHARFE 1996), Subadult (geboren 1994) bzw. Juvenil (geboren 1995; die Tibialängen wurden 3 Wochen vor dem Winterschlaf gemessen) zu bestimmen waren.

Die untere Intervallgrenze (25%-Quartil) der Adulten wurde der oberen Intervallgrenze (75%-Quartil) der Tibialängen der subadulten bzw. juvenilen Tiere gegenübergestellt (Abb. 1). In beiden Gebieten überlagerten sich die Quartilenintervalle nicht, so daß jeweils die Mitte zwischen dem 25%-Quartil der Adulten und dem 75%-Quartil der Subadulten und Juvenilen als Trennung zwischen Adult und Subadult bzw. Juvenil gewertet werden konnte. In beiden Gebieten ergab sich 1995 eine Trennung von Adult und Subadult bzw. Juvenil bei 35,2 mm Tibialänge.

Bei dieser Methode der Alterseinteilung ist allerdings zu beachten, daß das Wachstum der Tibia vom Nahrungsangebot beeinflußt sein kann. Die gleiche Auswertung für 1994 brachte etwas geringere Trennwerte (Laubwald: 34,0 mm; Nadel-Laubmischwald: 33,1 mm). Viele adulte Siebenschläfer von 1994 waren 1993 noch subadult und in dieser Phase ihrer körperlichen Entwicklung durch die außerordentlich schlechten Nahrungsbedingungen in 1993 (Ausfall der Buchen- und Eichenmast) gehemmt, wobei sich die ungünstigen Bedingungen im Nadel-Laubmischwald drastischer als im Laubwald auswirkten (SCHLUND 1996; SCHLUND und SCHARFE 1996). Demnach muß geprüft werden, ob der Trennwert von ca. 35 mm Tibialänge zwischen adulten und subadulten Siebenschläfern bei durchschnittlicher Futterverfügbarkeit auf andere Gebiete übertragen werden kann.

Die Trennung zwischen Subadulten und den Juvenilen drei Wochen vor dem Winterschlaf war über die Tibialänge nicht möglich (Abb. 1). Das Tibiawachstum der juvenilen,

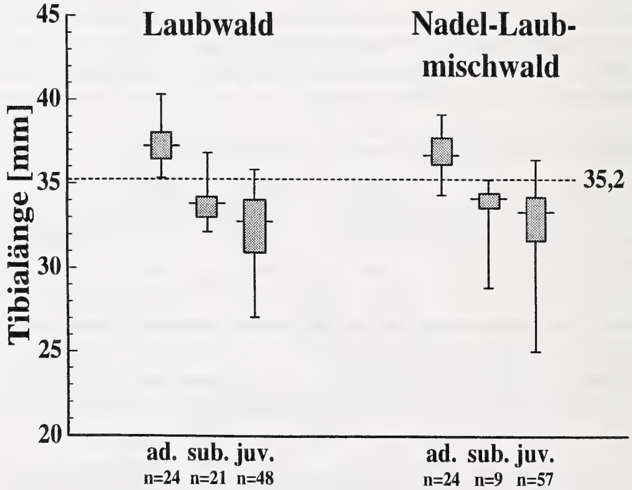


Abb. 1. Mediane, 25%- und 75%-Quartile sowie Maxima und Minima der Tibialängen von eindeutig adulten, subadulten und juvenilen Siebenschläfern von 1995 (n = Stichprobengröße, weitere Erläuterungen siehe Text).

in der Regel über 40 Tage alten Siebenschläfer ging zu diesem Zeitpunkt in einen asymptotischen Verlauf über (Abb. 2a) und näherte sich den Werten der subadulten Tiere an. Zwischen dem 10. und 40. Lebenstag war dagegen das Wachstum der Tibia linear zur Zeitachse. Außerdem unterschieden sich die Tibialängen der Juvenilen über diesen Zeitraum zwischen den Gebieten nicht (Mann-Whitney-U Test: z = 0,96, n = 206, n.s.). Das Ende

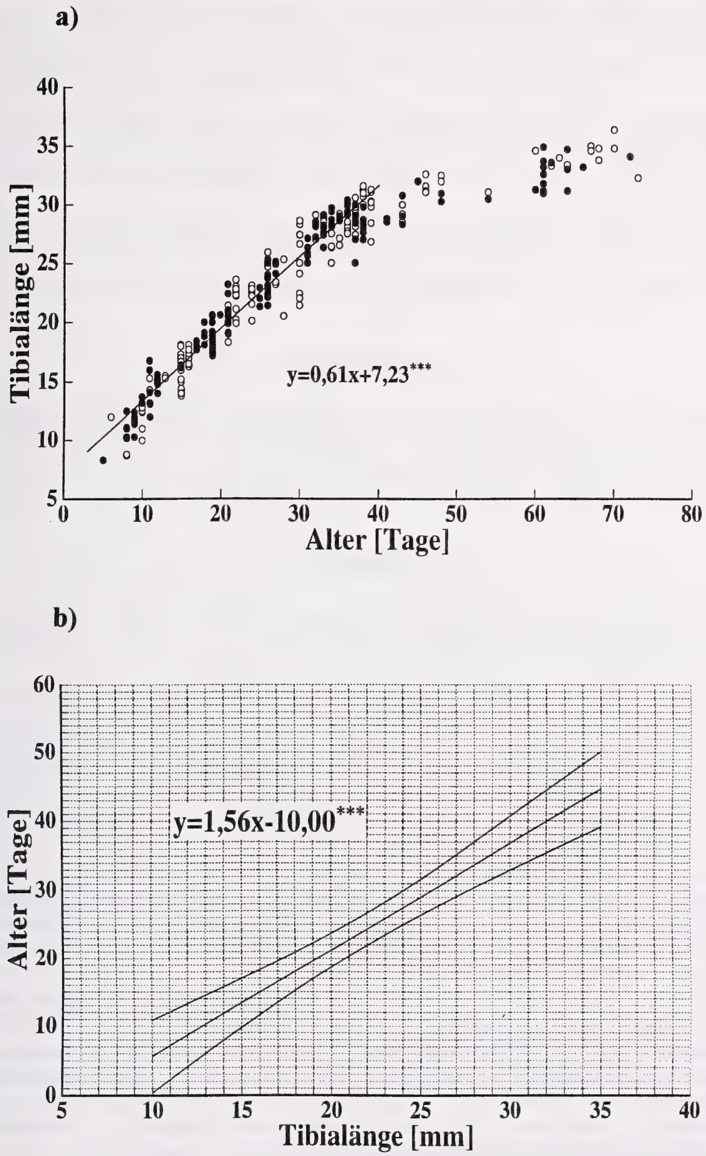


Abb. 2. (a) Entwicklung der Tibialänge von juvenilen Siebenschläfern in Abhängigkeit vom Alter. Die Regressionsgerade wurde bis zum 40. Lebenstag berechnet (Laubwald (●) und Nadel-Laubmischwald (○) jeweils zusammengefaßt. F = 4757,06, R^2 = 94,7, p < 0,001, n = 268.). (b) Altersbestimmung juveniler Siebenschläfer mit Hilfe der Tibialänge. Die Regressionsgerade wurde aus den Daten von Abb. 2a berechnet. Angegeben ist außerdem der 99%ige Vertrauensbereich der Regressionsgeraden.

des linearen Tibiawachstums lag bei einer Tibialänge von ca. 30 mm. In Abbildung 2 b ist das Alter der Juvenilen in Abhängigkeit der Tibialänge aufgetragen. Zusätzlich sind die 99%igen Vertrauensgrenzen der Regressionsgeraden (berechnet nach Sachs 1984) angegeben. Über die Tibialänge zwischen 10 und 30 mm kann demnach das Alter der jungen Siebenschläfer mit einer Genauigkeit von ±2 bis ±5 Tagen (je nach Länge der Tibia) bestimmt werden. Im Freiland wird dadurch eine schnelle Altersbestimmung der Neugeborenen während der Phase der Laktation (bis zum Alter von 30 Tagen) bzw. bis zum Selbständigwerden (ca. 45. Tag; Koenig 1960) möglich, ohne weitere Körpermerkmale wie z. B. den Entwicklungszustand von Händen, Augen oder Ohren überprüfen zu müssen (vgl. Koenig 1960; v. Vietinghoff-Riesch 1960). Über diesen Zeitraum sind auch gebiets- bzw. jahresspezifische, d. h. nahrungsbedingte Einflüsse auf die Entwicklung der Juvenilen weniger stark ausgeprägt, da die Mütter während der Phase der Laktation ungünstige Nahrungsbedingungen durch Verlust der eigenen Körpermasse ausgleichen können (Schlund 1996).

Die hier dargestellten Möglichkeiten der Tibialänge als Maß für die Körpergröße und zur Altersbestimmung sind in der vorliegenden Form nur für Siebenschläfer gültig. Die Methodik ist sicherlich aber auch auf andere Kleinsäugerarten übertragbar.

Danksagung

F. Scharfe, J. Fietz und M. J. Stauss danke ich für die Hilfe bei der Geländearbeit und für viele Anregungen bei der Auswertung der Daten. Dr. J. F. Burkhardt und Dr. J. U. Ganzhorn danke ich für hilfreiche Diskussionen und für die kritische Durchsicht des Manuskripts.

Literatur

Bieber, C. (1995): Ökologische Untersuchungen zur Populationsstruktur und -dynamik sowie zur Reproduktionsbiologie an drei Subpopulationen des Siebenschläfers (*Myoxus glis* L.). Diss., Phillips-Universität Marburg.

Hönel, B. (1991): Raumnutzung und Sozialsystem freilebender Siebenschläfer (*Glis glis* L.). Diss., Universität Karlsruhe.

Koenig, L. (1960): Das Aktionssystem des Siebenschläfers (*Glis glis* L.). Z. Tierphysiologie **17**, 427–505.

Nur, N. (1984 a): The consequences of brood size for breeding Blue Tits. I. Adult survival, weight change and the cost of reproduction. J. Anim. Ecol. **53**, 479–496.

Nur, N. (1984 b): The consequences of brood size for breeding Blue Tits. II. Nestling weight, offspring survival and optimal brood size. J. Anim. Ecol. **53**, 497–517.

Sachs, L. (1984): Angewandte Statistik. 6 Aufl. Berlin, Heidelberg: Springer Verlag.

Schlund, W. (1995): Individualmarkierung und Populationsbeobachtungen bei Siebenschläfern mit Hilfe von Transpondern. In: Methoden feldökologischer Säugetierforschung **1**. Ed. by M. Stubbe, A. Stubbe und D. Heidecke. Wissenschaftliche Beiträge/Martin-Luther-Universität Halle-Wittenberg, 345–354.

Schlund, W. (1996): Vergleich von Siebenschläferpopulationen (*Myoxus glis* L.) in zwei unterschiedlichen Waldgebieten. Diss., Eberhard-Karls-Universität Tübingen.

Schlund, W.; Scharfe, F. (1996): Unterschiede zweier Siebenschläferpopulationen (*Myoxus glis* L.) im Schönbuch in Abhängigkeit des Lebensraumes. Veröff. Naturschutz Landschaftspflege Bad.-Württ. **71/72**. (Im Druck.)

Vietinghoff-Riesch, A. Frhr. von (1960): Der Siebenschläfer (*Glis glis* L.). In: Monographien der Wildsäugetiere. Ed. by D. Müller-Using. Jena: Gustav Fischer Verlag Bd. 14.

Anschr. des Verf.: Dr. Wolfgang Schlund, Abt. Verhaltensphysiologie, Universität Tübingen, Beim Kupferhammer 8, D-72070 Tübingen

Z. Säugetierkunde 62 (1997) 191–192

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Buchbesprechungen

Hausser, J. (Hrsg.): **Säugetiere der Schweiz – Verbreitung, Biologie, Ökologie.** Denkschriften der Schweizerischen Akademie für Naturwissenschaften, Band 103. Basel, Boston, Berlin: Birkhäuser Verlag 1995. 501 pp., 90 Farbabb., 180 Farbkarten, Text deutsch, französisch und italienisch, geb. 78,– DM, 68,– sFr., 608,40 öS. ISBN 3-7643-5194-2.

Das vorliegende Werk über die Säugetiere der Schweiz wurde von der Schweizerischen Gesellschaft für Wildtierbiologie in der Reihe der Denkschriften der Schweizerischen Akademie der Naturwissenschaften herausgebracht. In seinem Einführungsartikel schildert der leitende Herausgeber Jaques Hausser die Ziele dieser Publikation und erörtert die mathematischen Methoden für die Analyse der Lebensräume der in der Schweiz vertretenen Säugetierarten. Es folgen Beiträge, an denen insgesamt 53 Spezialisten als Autoren beteiligt sind. Auch ausgestorbene Arten wie der Wolf (*Canis lupus*) und vom Menschen in die Schweiz eingeführte oder sich in das Land ausbreitende Arten wie Waschbär (*Procyon lotor*), Bisamratte (*Ondatra zibeticus*), Nutria (*Myocastor coypus*) oder das Sikawild (*Cervus nippon*) werden kurz behandelt.

Jede der zu behandelnden Ordnungen wird zunächst gekennzeichnet. Anschließend werden 88 Säugetierarten jeweils mit einem brillanten und informativen Farbphoto vorgestellt. Die Benennung der Arten erfolgt in allen vier Landessprachen, d. h. auch in Rätoromanisch. Für die neugeschaffene Schriftsprache Rumantsch Grischun wurden die entsprechenden Artnamen für diesen Band zusammengestellt. Im folgenden Abschnitt – jeweils eine Spalte mit gleichsinnigen Texten in Deutsch, Französisch und Italienisch – wird zunächst die Art kurz beschrieben, dann werden Bemerkungen zu ihrer Systematik gemacht; die Biologie der Art wird knapp und klar geschildert und der Lebensraum und die Verbreitung außerhalb der Schweiz werden charakterisiert. Die Verbreitung im Lande wird dann differenzierter erörtert. Dabei wird das relative Maß der „Marginalität" für den Höhenbereich, in dem die Spezies auftritt, herangezogen. „Wenn eine Art die Marginalität „0" für die Höhe aufweist, bedeutet das, daß der Durchschnitt der Beobachtungen dem Höhendurchschnitt der Schweiz entspricht. Wenn die Marginalität näher bei „1" liegt, kommt die Art lediglich in den tiefsten Lagen des Landes vor oder aber, im Gegensatz dazu, auf den höchsten Gipfeln" (S. 6). Die „Toleranz" einer Art für die Höhe wird anhand der Beziehung der Standardabweichung der tatsächlichen Artbeobachtungen zu derjenigen innerhalb des gesamten schweizerischen Territoriums ermittelt.

Besonders informativ sind die Karten am Ende jedes Art-Kapitels. In der Mehrzahl der Fälle werden jeweils zwei Karten geboten. Eine markiert das „potentielle Gebiet", in dem aufgrund der geographischen und ökologischen Gegebenheiten die Spezies in der Schweiz auftreten kann, die zweite bietet die tatsächlich nachgewiesene Verbreitung, welche durch Beobachtungen belegt werden konnte. Durch die Kennzeichnung jener Gebiete, in welchen eine Säugetierart vertreten sein könnte, bisher aber noch nicht nachgewiesen sein konnte, regen die Autoren zu fortführenden Felduntersuchungen an: „Diese Karten erlauben es, Kenntnislücken im Vorkommen der Art festzustellen und zukünftige Feldarbeiten gezielt durchzuführen" (S. XII). Zusätzliche Informationen werden für die Kleine Hufeisennase (*Rhinolophus hipposideros*) geboten: Auf den Seiten 82 und 83 werden ökologisch-historische Gesichtspunkte dargestellt; die Verminderung des potentiellen Verbreitungsgebietes dieser Art seit 1900 wird so in beunruhigender Weise anschaulich gemacht.

Zum Abschluß des Abschnittes mit den Artbeschreibungen werden noch drei Spezies (Etruskerspitzmaus – *Suncus etruscus*, Teichfledermaus – *Myotis dasycneme* und der Marderhund – *Nyctereutes procyonoides*) kurz behandelt, deren Anwesenheit in der Schweiz bisher nicht bestätigt werden konnte. Insgesamt sechs Anhänge, darunter ein Artregister und ein Literaturverzeichnis, machen die Materialfülle dieses Werkes gut zugänglich.

Das vorliegende Buch besticht schon beim ersten Durchblättern durch seine gediegene und schöne Aufmachung; auch die Tierabbildungen und der Text sind sorgfältig ausgewählt und klar und übersichtlich gedruckt. Zu dem gelungen Werk, welches seinen Preis wirklich wert ist, möchte der Referent den beteiligten Mammalogen, sowie der Schweizerischen Gesellschaft für Wildtierbiologie, seinen aufrichtigen Glückwunsch aussprechen!

P. Langer, Gießen

Kruuk, H.: **Wild Otters – predation and populations.** Oxford, New York, Tokyo: Oxford University Press 1995. 290 pp. £ 30.00 ISBN 0-19-854070-1

As in his previous monographs, the author gives a vivid description of his observations and presents the results of his investigations in a graphically very stimulating way. Actually, KRUUK presents a provisional final report of his long-term research work on the behaviour and the ecology of the otter on the peninsula Lunna, Shetland, and along the rivers Dee and Don, Scotland. In each chapter, he can therefore draw comparisons between the behaviour of the coastal otters in Shetland and the river otters in Scotland. Especially the chapters on spatial organization, social behaviour, diet, survival and mortality are worthy due to these possibilities of comparison and the long-term observations. The chapter on population structure covers over 30 pages. It can be read like a textbook on population biology, especially when KRUUK discusses several methods of data collection and then presents his results. Such a thorough data collection on otters does not exist elsewhere. The upper age limit of a female otter, for example, was found to be 15 years, but it should be noted also that after his sample analysis, most otters were estimated to die before the third year of life. While in Shetland otters are seasonally oestrous, they are oestrous throughout the year on the continent. KRUUK assumes that the seasonal occurrence of fish along the coast of Shetland is the reason for this difference. The fish-hunting strategies typical for this species could be observed on wild otters as well as on captured animals. Four otters were fitted with transmitters which gave data on body temperature, so that KRUUK and his colleagues were able to elicit information concerning the energetics of swimming and diving. In one of the last chapters, KRUUK makes a synthesis of all of his essential results and comes to the conclusion that in the case of the otter the resource dispersion hypothesis has little predictive value. Instead, the phylogeny of the social organization and the special hunting behaviour have led to the distribution pattern of otters along river banks.

The globally valid ideas, the welf-researched examples, the almost 300 literature citations – with over 30 publications by KRUUK himself and his team –, but also the last chapter on otter conservation make the book a most valuable buy not only for students of wildlife, but also for otter specialists. It presents a basis for discussion of and an argumentation for conservation of the otter and its bank habitats.

R. SCHRÖPFER, Osnabrück

Klevezal, G. A.: **Recording Structures of Mammals. Determination of Age and Reconstruction of Life History.** Translated and updated from original Russian edition 1988. Rotterdam and Brookfield, VT.: A. A. Balkema 1996. 274 pp.; Ned. Fl. 206,70. ISBN 90-5410-621-2.

Since the early 1950's, students of mammals have analysed regularly recurring layers in the teeth and bones of their subjects as indicators of absolute age. Validation has been possible using known age animals raised in captivity, from marked and subsequently recaptured animals, or by marking the hard structures with intra-vitam dyes or fluorescing substances such as teracycline. From this, annual, lunar and even diel layers have been recognised. The process continues. Thus, MIRIAM MARMONTEL 1995 (in Population Biology of the Florida Manatee, U.S. Dept. of the Interior, Nat. Biol. Survey, Information and Technology Rept. 1, pp. 98–119) could not use teeth to age *Trichechus manatus longirostris* because these are replaced forwards through life, as in elephants. She found growth layer groups in the dome portion of the tympano-periotic bone complex, established their periodicity from animals held since birth which died, and went on to calculate reproductive and mortality rates for the Florida population. The basis of separation of dentinal tooth layers is varying optical density, seen either in thin undecalcified sections or in decalcified stained sections. Whether the changes in density are due to changes in mineralisation or in the organic matrix is still not clear. However, seasonal changes in growth of the tooth relate directly to seasonal changes in body growth, which in turn relate to the external climatic cycle: most tooth growth in mammals inhabiting temperate terrestrial habitats takes place in a fairly short spring-summer period. In bone tissue, growth zones are ended by resting lines. This is a most thorough and timely review of the subject. The English translation (by V. MINA and A. V. OROSHKIN) is good enough that there are a few ambiguities of meaning.

D. E. SERGEANT, Hudson Hts., Quebec

Redaktionelle Hinweise

Einsendung und Annahme von Manuskripten: Ms. zur Veröffentlichung sind einzusenden an den 1. Schriftleiter: Herrn Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel. e-mail: dkruska@ifh.uni-kiel.de

Über die Annahme von Ms. zur Veröffentlichung wird gemäß Geschäftsordnung der Deutschen Gesellschaft für Säugetierkunde entschieden. Der Eingang von Ms. wird sofort bestätigt, und nach Erhalt der Gutachten werden die Autoren über die Entscheidung umgehend informiert.

Schriftwechsel, der die technische Drucklegung betrifft, ist zu richten an: Zeitschrift für Säugetierkunde, Gustav Fischer Verlag, Villengang 2, D-07745 Jena.

Äußere Form der Manuskripte: Die Ms. sind 3fach und vollständig als Original mit 2 Kopien in deutscher oder englischer Sprache einzureichen. Sie müssen mit Schreibmaschine oder als deutlich lesbare Computerausdrucke auf DIN A4-Blättern (21 × 29,7 cm), mit einem linken Heftrand von 4 cm und durchgehend mit einem doppelten Zeilenabstand geschrieben sein. Jedes Ms. soll auf der 1. Seite folgende Angaben enthalten: Titel der Studie; Name(n) der Autoren (männliche Vornamen nur in Initialen, weibliche ausgeschrieben); Institution(en), an der (denen) die Studie durchgeführt wurde. Ferner soll bei längeren Titeln ein kurzer Kolumnentitel (Seitenüberschrift) von maximal 72 Anschlägen angegeben werden.

Die Schrifttypen müssen einheitlich sein, ohne halbfette, gesperrte, kursive etc. Hervorhebungen. Fußnoten auf den Seiten oder Appendices am Ende sind nicht zugelassen. Autorennamen im Zusammenhang mit Literaturzitaten sind im Text mit Bleistift zu unterstreichen. Wissenschaftliche zoologische und botanische Gattungs-, Art- und Unterartnamen sind mit einer Schlangenlinie zu unterstreichen. Der Name von Erstbeschreibern bei wissenschaftlichen Namen wird nicht unterstrichen.

Im Ms. ist am Rand mit Bleistift zu vermerken, an welcher Stelle die einzelnen Abbildungen und Tabellen eingefügt werden sollen.

Am Ende der Studie, im Anschluß an das Literaturverzeichnis, sind die genauen postalischen Adressen des (der) Autoren anzugeben.

Umfang und Aufbau der Manuskripte: Manuskripte können als Originalarbeiten oder als wissenschaftliche Kurzmitteilungen veröffentlicht werden.

a) Originalarbeiten: Originalarbeiten sollen einschließlich Abbildungen, Tabellen und Literaturverzeichnis einen Gesamtumfang von 30 Ms.-Seiten nicht überschreiten. Der Text soll eine klare Gliederung aufweisen in: Abstract (in englischer Sprache), Einleitung, Material und Methode, Ergebnisse, Diskussion (oder zusammengefaßt als Ergebnisse und Diskussion), Danksagungen, Zusammenfassung und Literatur.

Bei deutschsprachigen Studien ist über dem englischen Abstract der Titel in englischer Sprache anzugeben. Bei englischsprachigen Studien ist entsprechend über der deutschen Zusammenfassung der Titel in deutscher Sprache anzugeben.

b) Wissenschaftliche Kurzmitteilungen: Wissenschaftliche Kurzmitteilungen sollen einen Gesamtumfang von 5 Ms.-Seiten nicht überschreiten. Sie enthalten kein Abstract und keine Zusammenfassung. Bei deutschsprachigen Ms. ist jedoch auf der 1. Seite zusätzlich eine englische Übersetzung des Titels anzugeben, bei englischsprachigen entsprechend eine deutsche Übersetzung. Wissenschaftliche Kurzmitteilungen sind äußerlich nicht in die Kapitel Einleitung, Material und Methode, Ergebnisse und Diskussion gegliedert, müssen aber in der textlichen Darstellung diese Strukturierung erkennen lassen.

Abbildungen: Anzahl und Größe der Abbildungen sind unbedingt auf das notwendige Mindestmaß zu beschränken. Es können nur kontrastreiche, reproduktionsfähige Originale verwendet werden, farbige Abbildungen werden nicht angenommen. Beschriftungen müssen einheitlich und wegen späterer Verkleinerung groß und kräftig sein. Auf der Rückseite sind laufende Numerierung, Zeitschrift und Autorennamen anzugeben. Alle Bildunterschriften sollen auf einem gesonderten Blatt gelistet werden.

Tabellen: Tabellen müssen auf ein Mindestmaß beschränkt werden. Jede Tabelle muß auf einem gesonderten DIN A4-Blatt angelegt sowie mit Überschrift und laufender Numerierung versehen sein. Umfangreichere Tabellen müssen auf Folgeblättern als Fortsetzung erscheinen.

Literaturverzeichnis: Jede zitierte Arbeit ist in alphabetischer Reihenfolge aufzuführen. Es soll nur international erreichbare Literatur zitiert werden. Die Zeitschriften werden mit ihrem Kurztitel angegeben.

Beispiele:

a) Zeitschriftenbeiträge:

KALKO, E. K. V; HANDLEY, C. O. JR. (1994): Evolution, biogeography, and description af a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá. Z. Säugetierkunde **59**, 257–273.

b) Bücher:

HERRE, W.; RÖHRS, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.

c) Handbuchbeiträge:

NIETHAMMER, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. NIETHAMMER und F. KRAPP. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

Drucklegung: Der jeweilige Hauptautor erhält sowohl die Andrucke der Bilder zur Prüfung wie auch den kompletten Umbruch seines Artikels zusammen mit dem Ms. Es dürfen nur tatsächliche Satzfehler korrigiert werden. Vom Ms. abweichende Änderungen werden dem Autor in Rechnung gestellt. Es sind die üblichen Korrekturzeichen zu verwenden. Ein als druckfertig bezeichneter Abzug ist zu senden an: Herrn Prof. Dr. Peter Langer, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität, Aulweg 123, D-35385 Giessen. e-mail: peter.langer@anatomie.med.uni-giessen.de

Sonderdrucke: Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen erhalten 50 Sonderdrucke gratis. Mehrbedarf kann gegen Berechnung bei Rücksendung des Umbruchs bestellt werden.

Publisher: Gustav Fischer Verlag GmbH & Co. KG, Branch Office Jena, P. O. Box No. 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/6 26-3; Fax ++49(0)36 41/62 65 00; e-mail: office.j@gfischer.de
Advertisement bookings: Enquiries should be directed to Gustav Fischer Verlag, Advertising Manager: Sabine Schröter, P. O. Box 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/62 64 28, Fax ++49(0)36 41/62 64 21
Advertising rates: The price list from February 1, 1997 is effective at present.
Distribution and subscription agency:
For customers **in the German speaking countries:** Please turn to your bookshop or to SFG-Servicecenter Fachverlage GmbH, Zeitschriftenvertrieb: Barbara Dressler, Villengang 2, D-07745 Jena, Germany. Phone ++49(0)36 41/62 64 44, Fax ++49(0)36 41/62 64 43;
For customers **in all other countries:** Please contact your bookshop or Stockton Press., c/o Debbie Floyd, The Subscription Dept., Houndmills, Basingstoke, Hants RG 21 6XS, UK. Phone ++44(0)12 56/35 18 98. Fax ++44/12 56/32 83 39. Subscribers in the **USA** can call toll free on ++1/800/747 3187.
Terms of delivery (1997): 1 volume consisting of 6 issues.
Subscription rate (1997): Price per volume: DM 398.00; ÖS 2 906.00; sFr 382.50; UK Sterling 183.00
Single issue price: DM 80.00; ÖS 584.00; sFr 77.00; UK Sterling 35.00
Reduced membership rates are available on request. Please turn to our publ. house.
All prices mentioned above are exclusive postage. USdollar prices are converted at the current exchange rate. We accept the following credit cards: VISA/Mastercard/American Express, (Please note card-No. and expiry date).
Banking connections:
For customers in the **German speaking countries:**
Deutsche Bank AG Jena, Konto-Nr. 6 284 707, BLZ 820 700 00.
For costumers **in the other countries:**
UK Post Office Giro Account No. 5 192 455. Full details must accompany the payment.
All prices are subject to change without notice.
Subsciption information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting, printing and binding: druckhaus köthen GmbH
Printed in Germany

Abstracted/Indexed in
Animal Breeding Abstracts; Current Contents Agriculture, Biology Environmental Sciences; Biological Abstracts; *BIOSIS* database; Current Advances in Ecological and Environmental Sciences; Dairy Science Abstracts; Fisheries Review; Helminthological Abstracts; Index Veterinarius; South Pacific Periodicals Index; Veterinary Bulletin; Key Word Index to Wildlife Research; Wild Review (Fort Collins); Zoological Record

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

GUSTAV FISCHER

ISSN 0044-3468
Z. Säugetierkunde
Jena · 62(1997)4 · S. 193-256
August 1997

4
1997

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **62** (1997) 193–202

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Evidence for specific independence of the shrew (Mammalia: Soricidae) of St. Paul Island (Pribilof Islands, Bering Sea)

By R. L. RAUSCH and VIRGINIA R. RAUSCH

Department of Comparative Medicine, University of Washington, and Burke Memorial Washington State Museum, Seattle, Washington, U.S.A.

Receipt of Ms. 30. 07. 1996
Acceptance of Ms. 18. 02. 1997

Abstract

The authors define the karyotype (2n 55, NFa 62) of the shrew (subgenus *Otisorex*) inhabiting St. Paul Island (Pribilof Islands), Bering Sea, and present data concerning relationships of that taxon. The somatic chromosomal complement (male) comprised 26 pairs of homologous autosomes, the sex chromosomes X and Y, and one additional chromosome, the smallest of the complement, for which no homologue was identified. The function of this unpaired element is uncertain; that it may be involved in the sex-chromosome system is suggested (a Y_2 has not been recorded in any shrew of the subgenus *Otisorex*). The applicable name for the shrew of St. Paul Island has been questionable for many years and thought to be *Sorex hydrodromus* Dobson, 1889, the problem in part due to imprecise data regarding the type specimen of *S. hydrodromus.* Although type locality for *S. hydrodromus* was given as Unalaska Island (Aleutian Islands, Bering Sea), where no shrew is known to exist, there is evidence that the original specimens were collected somewhere within the rather vast region that formed the governmental unit called Unalaska District by the administrators of Russian America (prior to 1867). The District included the western end of the Alaska Peninsula, the eastern Aleutian Islands, and the Pribilof Islands. That *S. hydrodromus* in dentition is compatible with shrews of the *S. araneus* group (subgenus *Sorex*) has been indicated in the literature. We conclude that the applicable name for the shrew of St. Paul Island is *Sorex* (*Otisorex*) *pribilofensis* Merriam, 1895. The karyotype of *S. pribilofensis* and other taxonomic characters distinguish that species from the three Eurasian members of subgenus *Otisorex*, as well as from all nearctic species for which pertinent data exist. With the exception of that shrew and one species of rodent, the indigenous terrestrial mammals occurring on islands in the Bering Sea differ only subspecifically from those on the two continents. The authors suggest that the precursor of *S. pribilofensis* became established in Beringia during pre-Würm time.

Introduction

The Recent mammalian faunas of the islands in the Bering Sea, within the limits of the former Beringia, consist of species that evidently had occupied highlands that became isolated by rising sea-levels at intervals during Pleistocene time and were able to persist under consequent ecological and spatial constraints. Of the six major islands in the Bering Sea, the four most remote, St. Paul, St. George, St. Matthew, and Hall, have only single species of indigenous mammals (not including the arctic fox, which migrates to and from the islands on the sea-ice, and the polar bear, which formerly was present on some islands during summer). Individuals of other species are carried rarely on drifting ice to St. Lawrence Island. The red fox occurs on Nunivak Island (separated from the Yukon-Kuskokwim river delta on the Alaskan mainland by 30 km-wide Etolin Strait), and probably also freely moves over sea-ice. Three families of small mammals (indigenous) are re-

presented on the Bering Sea Islands: Soricidae, Sciuridae, and Arvicolidae. Four species are holarctic, two are Beringian endemics, and one is nearctic (cf. Rausch and Rausch 1995). In addition, one species, the shrew occurring on St. Paul Island, Pribilof Islands (57°10′ N, 170°15′ W) has been of uncertain identity.

Shrews are present on three of the Beringian islands. *Sorex cinereus hollisteri* Jackson occurs on Nunivak Island, as well as in continental Alaska; the insular population is distinguished by a pale to nearly white pelage. *Sorex cinereus jacksoni* Hall et Gilmore is limited to St. Lawrence Island. The shrew on St. Paul Island has been designated either *Sorex hydrodromus* Dobson or *Sorex pribilofensis* Merriam; herein, we follow the nomenclature applied by van Zyll de Jong (1982, 1991), designating the species as *S. pribilofensis. Sorex cinereus* Kerr and the shrew of St. Paul Island are referable to the subgenus *Otisorex*. In the present report, we describe the karyotype and discuss macromorphologic characteristics of *S. pribilofensis* as well as its status with respect to other amphiberingian species.

Material and methods

During August 1995, we collected three shrews on St. Paul Island (one subadult male, one subadult female, one adult female). Skins and complete skeletons were prepared, and reproductive organs were preserved in 10 per cent formalin solution. Those organs and dental and cranial features were studied by means of a stereoscopic microscope with ocular micrometer graduated in tenths of millimeters. (Skulls from 14 animals and reproductive organs from 2, collected in other years, were useful for comparison.) For definition of the karyotype, cells from marrow and lymphatic tissue were treated with colchicine and hypotonic solution, centrifuged, fixed, and placed on slides; they later were stained in the laboratory at the University of Washington, applying the method of Seabright (1972) for G-banding and that of Sumner (1972) for C-banding. Cells from testes were fixed and stained in acetic orcein. Chromosomes were counted and evaluated in intact cells in metaphase. The karyograms were prepared on the basis of photographs of 10 cells from the male shrew, and by comparison of chromosomes in cells of the three animals.

Measurements of chromosomes were obtained according to the method of Levan et al. (1964). For the karyograms, arm-ratio and size were the bases for assembling pairs of non-banded chromosomes; those with G-bands were identified from banding-pattern and size, and C-banded chromosomes were distinguished by size and by location of centromeric heterochromatin. The sex-chromosomes were determined by differential characteristics. The fundamental number (FN) of chromosomal arms was established following the method of Matthey (1945).

Voucher-specimens have been deposited as follows: Burke Memorial Washington State Museum, University of Washington, No. 39 491; and Museum of Southwestern Biology, University of New Mexico, Nos. 83 326 and 83 327.

Morphometric data for shrews of the *Sorex cinereus* group are not included herein; extensive analyses have been published by van Zyll de Jong (1982, 1991).

Results

The chromosomal preparations from the male shrew included many intact cells in metaphase, in each of which 2 n was 55: 52 autosomes, plus the sex-chromosomes (X and Y), and an additional chromosome for which no homologue was identified. Based on arm-ratio in metaphase, 8 large and 2 very small autosomes were classified as metacentric to submetacentric (range of arm-ratio 1.04 to 2.90); those of the remaining autosomal complement were classified as subtelocentric to acrocentric (range of arm-ratio 2.95 to 10.00) (four of that group, with lower arm-ratios, were perhaps marginally submetacentrics). The X-chromosome was relatively large and submetacentric (arm-ratio 1.88 to 2.75); the Y-chromosome, of intermediate size, was subtelocentric (arm-ratio 2.95 to 4.50). The un-

Fig. 1. Karyogram of *Sorex pribilofensis*, male. Standard Giemsa stain. Scale-bar represents 5 micrometers.

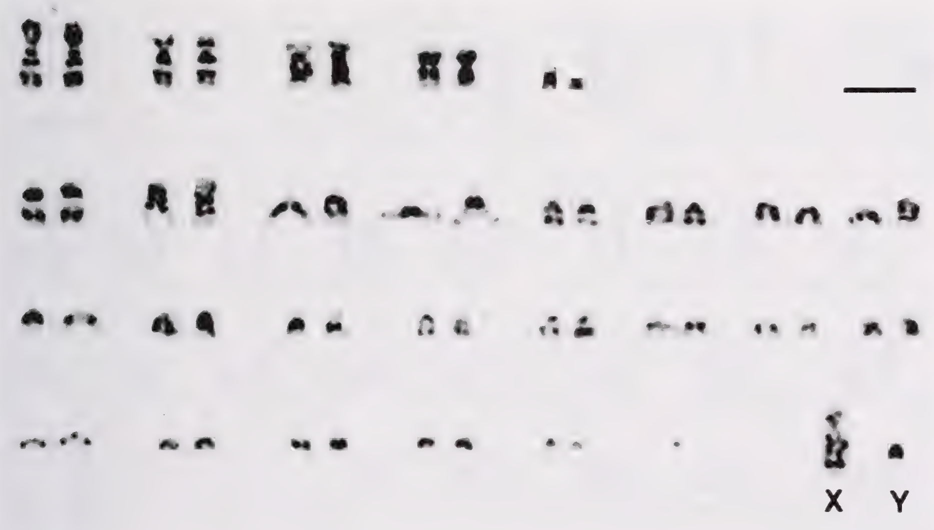


Fig. 2. Karyogram of *S. pribilofensis*, male, G-banded. Arrangement of chromosomes as in Fig. 1. Scale-bar represents 5 micrometers.

paired chromosome was very small and could not be measured with accuracy, although with the microscope at maximal magnification, short arms were discernible, indicating subtelocentric form. In the karyograms (Figs. 1–4), the complements of four cells, with staining as indicated to show characteristics of the individual elements, are arranged by size and conformation: meta/submetacentric autosomes, Nos. 1–10; subtelo/acrocentric autosomes, 11–52; the unpaired chromosome (No. 53) has been placed last, with the autosomes. The X-chromosome evidently was negative for heterochromatin, as were the short

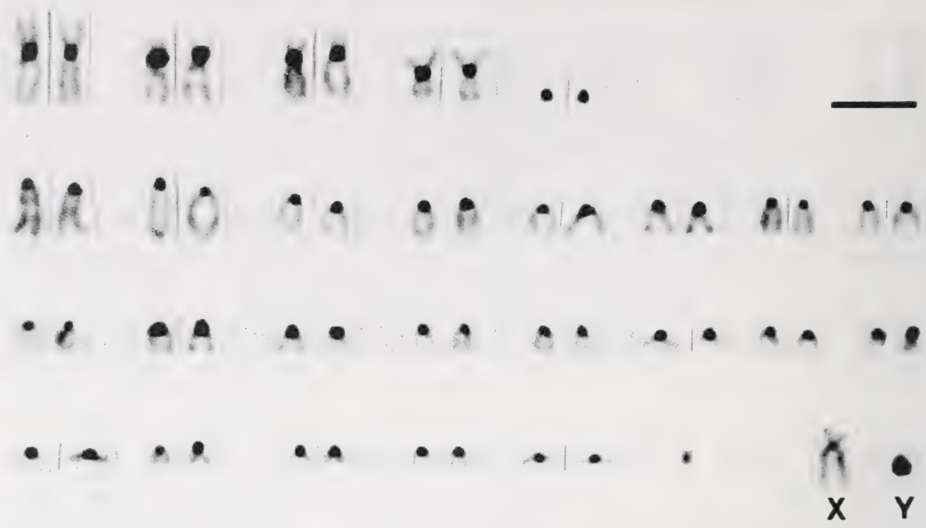


Fig. 3. Karyogram of *S. pribilofensis*, male, C-banded. Arrangement of chromosomes as in Fig. 1. Scale-bar represents 5 micrometers.

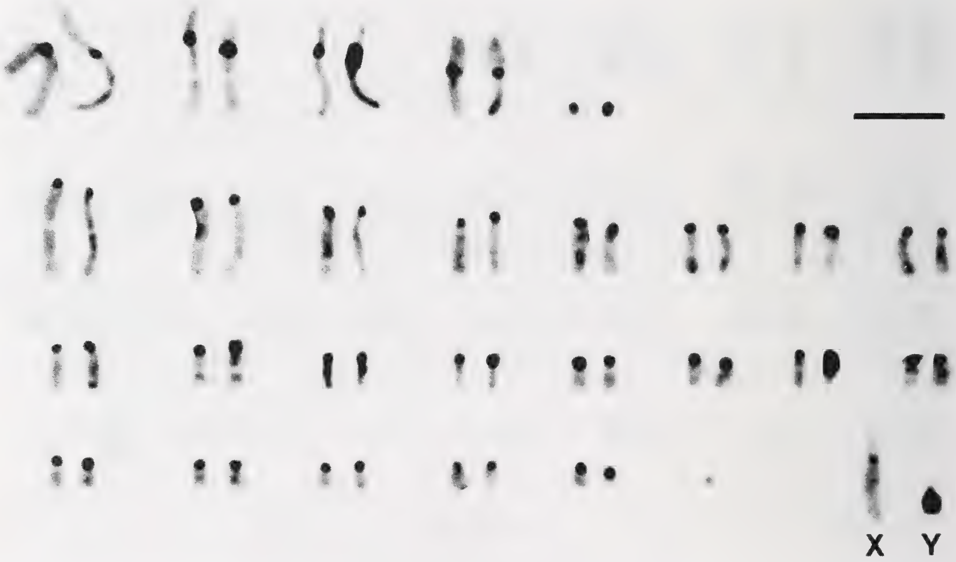


Fig. 4. Karyogram, *S. pribilofensis*, male, C-banding of chromosomes in early metaphase. Arrangement of chromosomes as in Fig. 1. Scale-bar represents 5 micrometers.

arms of the Y-chromosome, and the entire unpaired element. The FN (autosomes, not including chromosome No. 53) was 62. The cultured cells from the two female shrews did not provide preparations of adequate quality and only selected chromosomes could be compared with those of the male; the female diploid number was not certainly determined. In the testicular cells, we found neither mitotic nor meiotic divisions. The significance of chromosome No. 53 was not established.

The adult female was not lactating but had earlier produced young; the uterine cornua, with 5 placental scars on right and 4 on left, were about 2 mm in diameter and each was 8–9 mm in length; length of the vagina was approximately 3.5 mm. The glans penis (adult male) was 1.2 mm in length and 1.5–1.6 mm in width. In lateral view, the anterior surface was truncate, sloping ventrad; the orifice of the urogenital duct on that surface was not discerned. A corona was lacking.

Dentition of all specimens examined corresponded closely with the descriptions and figures of MERRIAM (1895) and JACKSON (1928) for *S. pribilofensis*. The medial tines of the incisors in our material were prominent (about 0.25 mm long when unworn); in form and position, they were much like those of *S. cinereus*.

Discussion

The subgenus *Otisorex* is represented in Eurasia by only three species (PAVLINOV and ROSSOLIMO 1987): *Sorex leucogaster* Kuroda, 1933 (syn. *S. beringianus* Yudin, 1967) (type locality: Paramushir Island, Kuril Islands); *S. portenkoi* Stroganov, 1956 (type locality: vicinity of Anadyr', Chukotka); and *S. camtschaticus* Yudin, 1972 (type locality: Kambal' Bay, Kamchatka). The taxonomic status of those species has been discussed in detail (RAUSCH and RAUSCH 1995). *Sorex pribilofensis* (2 n 55, FNa 62) is distinct karyotypically from two of the three species of the subgenus *Otisorex* that occur in Eurasia. The karyotype of *S. leucogaster* (2 n 66, FN 70) resembles that of *S. cinereus*; the diploid number of *S. portenkoi* is 60, FN 60 (IVANITSKAIA and KOZLOVSKII 1985). The karyotype of *S. camtschaticus* has not been defined. That taxon was described originally as a subspecies of *S. cinereus* and is distinguished by large size, long tail, and cranial characteristics (YUDIN 1972). Well developed fringes of bristle-like hairs laterally bordering the hind feet are present (YUDIN 1973). Neither the glans penis nor dentition of *S. camtschaticus* was described by YUDIN as notably different; presumably, they closely resemble those of *S. cinereus*. The morphometric analyses of VAN ZYLL DE JONG (1982, 1991) support the conclusion that *S. camtschaticus* is an independent species.

The karyotype of *S. pribilofensis* is unlike any known for the subgenus *Otisorex*. In other taxonomic characters as well, the St. Paul Island shrew differs from members of the subgenus occurring at the present time in Alaska (RAUSCH and RAUSCH 1995). Only two of those, *S. cinereus* and *S. monticolus* Merriam, are known to have extensive geographic ranges in northwestern North America. *S. c. cinereus* Kerr and *S. c. hollisteri* occur widely in Alaska. *S. monticolus* is represented on the Alaskan mainland by three subspecies; one, *S. m. shumaginensis* Merriam, also inhabits the Shumagin Islands, which are not in Bering Sea but lie near the southern shore of the lower Alaska Peninsula. The patterns of their distribution suggest that the other members of the subgenus *Otisorex* occurring in Alaska dispersed into northwestern North America during post-glacial time; well defined taxonomic characters distinguish each of them from *S. pribilofensis*. (Other nearctic species of subgenus *Otisorex*, evidently also distributed to the south of the continental glacier during Würm/Wisconsin time, are not considered here.)

We were not able to discern karyotypic relationships of *S. pribilofensis* on the basis of Robertsonian chromosomal rearrangements nor of interspecific chromosomal homologies. As in *S. cinereus* (2 n 66, FNa 70), two small submetacentric autosomes were present, and centromeric heterochromatin was present in all autosomes. In the two species, the sex-chromosomes (X and Y) appeared to be similar. In *S. pribilofensis*, the "unpaired" chromosome (No. 53) may be also a sex-chromosome, perhaps Y_2. If so, for the subgenus *Otisorex*, it would be unique.

The uterus of some shrews of the subgenus *Sorex* has been described by DOLGOV and LUK'IANOVA (1966), but little is known of the form of the organ in members of the subge-

nus *Otisorex*. In the adult female *S. pribilofensis*, the uterus resembled that of *S. cinereus* as illustrated by Yudin (1972) and as we observed in three specimens. The glans penis of *S. pribilofensis* also somewhat resembled that of *S. cinereus*. The glans of "*S. hydrodromus*" was described by Yudin (1969) from a shrew labeled as from "Unalaska Island"; he reported that the organ was 2 mm in length and only 0.7 mm in diameter at the base; the urogenital orifice was within an anterior concavity, enclosed by a peripheral ridge. His illustration (Yudin 1969) indicated that the organ resembled that of *S. pribilofensis*. Yudin (1969) studied the type specimen of *S. hydrodromus* (No. 2389, a female) in the Museum at Leningrad; he did not provide the number of the male specimen he examined.

The applicable name for the species of shrew occurring on St. Paul Island, and its systematic status, have remained uncertain due in part to problems relative to accession numbers of museum-specimens, type locality, and discrepancies in reported descriptions of the dentition and other anatomical characters. A taxon believed to have represented that species was described as *Sorex hydrodromus* by Dobson (1889) on the basis of a specimen in the Zoological Museum of the Russian Imperial Academy of Sciences, St. Petersburg, for which type locality was given as Unalaska Island (Aleutian Islands). The Museum's accession number was not listed by Dobson (1889) but was stated to have been No. 85 by Jackson (1928). Dobson (1889) remarked that the teeth closely resembled those of *Sorex vulgaris* (= *S. vulgaris* Nathusius, 1838 = *S. araneus* L.), and he considered also that the shrew was aquatic, having pedal fringes even more developed than those of *Crossopus fodiens* [= *Neomys fodiens* (Pennant)]. Evidently, the specimen studied by him cannot now be certainly recognized in the collections of the Zoological Museum. On the basis of Dobson's (1889) description and figure of the rostrum and teeth of *S. hydrodromus*, Jackson (1928) listed it as an independent species, but indicated its close similarity to *S. tundrensis* Merriam (*arcticus* group). Jackson (1928) provided a detailed description of *S. pribilofensis*, which he placed in a distinctive group.

At the Zoological Museum also, Hall (in Murie 1959) found the assumed type of *S. hydrodromus* to be an immature female, No. 2389 (Zoological Museum of the Academy of Sciences, Leningrad, U.S.S.R.), collected by I. G. Voznesenskii at "Unalaska", during the period 1840–1848. That specimen and a second *S. hydrodromus* from "Unalaska" (No. 2370) he noted were distinct from specimens of *S. pribilofensis* (Nos. 2437 and 2485, one labeled as collected by Voznesenskii on St. Paul Island) (Hall, in Murie 1959), and he concluded that *S. hydrodromus* was a member of the *S. arcticus* group of shrews. Hoffmann and Peterson (1967) considered that specimens of *S. hydrodromus* were virtually indistinguishable from *S. pribilofensis*, and proposed, in view of the problems concerning types and localities, that the designation *hydrodromus* be suppressed in favor of *pribilofensis* for the species from St. Paul Island.

Those decisions notwithstanding, the uncertainty about the status of *S. hydrodromus* and *S. pribilofensis* has persisted and published opinions concerning it have become increasingly divergent, as shown by the following (a complete review of the numerous Russian literature is not given here). Hall and Kelson (1959) recognized *S. pribilofensis* and listed *S. hydrodromus*, in agreement with Jackson (1928) that it might prove to be identical with "*Sorex arcticus tundrensis*". Yudin (1969) did not favor synonymy for *pribilofensis* until additional taxonomic characters could be compared. Gureev (1979) listed *S. pribilofensis* as an independent species and suggested that *S. hydrodromus* be placed in synonymy with *S. cinereus*. Corbet and Hill (1980) accepted *S. pribilofensis* and did not list *S. hydrodromus*. Junge and Hoffmann (1981) applied the name *S. hydrodromus* to the shrew of St. Paul Island. Hall (1981) listed *S. pribilofensis* as a synonym of *S. hydrodromus*, as did Honacki et al. (1982). Van Zyll de Jong (1982, 1991) designated the shrew on St. Paul Island as *S. pribilofensis*, in the subgenus *Otisorex*. Hutterer (1993) stated that *hydrodromus* is the applicable name for that taxon, on grounds of priority.

S. pribilofensis was applied by RAUSCH and RAUSCH (1995). In a major work on insectivores of Siberia (YUDIN 1989), it was concluded that *S. hydrodromus* and *S. cinereus camtschatica* (= *S. camtschaticus*) are very similar and that the morphological differences between them are compatible with the wide range of variation exhibited by *S. cinereus*. (That volume, published by his colleagues three years after the untimely death of B. S. YUDIN, unfortunately omitted some of the recent Russian literature concerning shrews of subgenus *Otisorex*.)

A major question relating to the status of the taxon designated *S. hydrodromus* is the identification of its type locality, which was recorded as "Unalaska" on specimen-tags by the collector, I. G. VOZNESENSKII, circa 1840 (HALL, in MURIE 1959). The locality "Unalaska" has been judged to mean Unalaska Island, but numerous attempts to find shrews there have been unsuccessful, and the Aleut residents have never recognized that any shrew occurs on the island (see PETERSON 1967). Small mammals of two species, a vole, *Microtus oeconomus* (Pallas), and a varying lemming, *Dicrostonyx unalascensis* Merriam, are resident there, however, and at intervals each attains high numerical density. In a written communication, A. A. GUREEV stated (in PETERSON 1967) that a memorandum in the Russian archives, dated 1842, mentioned two mammals collected on Unalaska Island that were thought to correspond to the two shrews labeled as from "Unalaska". If VOZNESENSKII (see HALL, in MURIE 1959) had opportunity to collect only two mammalian specimens on the Island, it is conceivable that they may have represented one or both species of the arvicolids. PETERSON (1967) noted that the designation "Unalaska", as applied by the collector, could have referred to the Russian American "Unalaska District", which encompassed the entire region from the Shumagin Islands at the western end of the Alaska Peninsula, westward to the Fox Islands, and the Pribilof Islands (see GOLOVIN 1862; DALL 1870). The Alaska Peninsula and Unimak Island, the Aleutian Island closest to the mainland, have a continental mammalian fauna, and shrews of at least three species (*S. cinereus*, *S. monticolus*, and *S. tundrensis*) could have been collected within the Unalaska District, in addition to that on St. Paul Island (in the same district). HALL (in MURIE 1959) gave data for four shrews: No. 2389, type of *S. hydrodromus*, Unalaska: No. 2370, *Sorex*, Unalaska, also identified as *S. hydrodromus*; No. 2437, *Sorex pribilofensis*, St. Paul Island; and No. 2485. HALL (in MURIE 1959) stated that Nos. 2485 and 2437 originated on St. Paul Island; evidently both had been so labeled by the collector. HALL's descriptions (in MURIE 1959) indicate that the pigmentation on the cingula of the unicuspids of specimens identified as *hydrodromus* was not compatible with its allocation to the subgenus *Otisorex*, as compared with the specimens from St. Paul Island.

In *S. pribilofensis*, we found the five unicuspids to be graded in size, from the largest (anteriormost) to the smallest (posteriormost), and the first unicuspid slightly longer than the posterior cusp of the incisor; the opposite was shown in *S. hydrodromus* (DOBSON 1889). YUDIN (1969) also studied specimen No. 2389, and reported that the posterior cusp of the incisor, as in *pribilofensis*, was shorter than the first unicuspid, but the unicuspids were not similarly graded. In the posthumous volume of YUDIN (1989), the relative lengths of unicuspids of *S. hydrodromus* (specimen-number not given) did not correspond with his earlier (YUDIN 1969) description but exhibited a gradation in length similar to that of *S. pribilofensis* as seen in our material.

VAN ZYLL DE JONG (1982) did not place *S. pribilofensis* in synonymy with *S. hydrodromus*, in view of the substantial doubt existing with regard to the identity of the type of *S. hydrodromus*. He further considered that his comparisons of tail-lengths alone indicated that *S. hydrodromus* and *S. pribilofensis* could not be derived from the same soricid population. His data made clear that the tail-length of *S. hydrodromus* was more than six standard deviations from the mean for *S. pribilofensis*. In agreement with VAN ZYLL DE JONG (1982), we retain the designation *Sorex pribilofensis* for the shrew on St. Paul Island. For the specimens of *S. hydrodromus* in St. Petersburg, stated to have been preserved in

alcohol, DNA analysis may be a possibility. We attribute significance to the judgements of Jackson (1928) and Hall (in Murie 1959) that the specimens designated *S. hydrodromus* represent a member of the *Sorex araneus* group.

The Pribilof Islands lie in the Bering Sea quite near the southern edge of the continental shelf. During the maxima of the last (Würm/Wisconsin) and penultimate (Riss/Illinoian) glacial periods, the present islands existed as highlands on the exposed continental shelf. Sea-level fell probably about 135 m in the Bering Sea during the maximal phase of the penultimate glaciation (Hopkins 1973). Evidence of glaciation of pre-Würm age exists on St. George Island but not on St. Paul Island (Hopkins and Einarsson 1966). Terrestrial mammals inhabiting islands in the Bering Sea with two exceptions represent species of extensive geographic ranges in Beringia during the last glaciation; they differ only subspecifically from Recent species. Two species, *Sorex pribilofensis* and a varying lemming, *Dicrostonyx exsul* Hall et Gilmore on St. Lawrence Island, evidently are of pre-Würm origin, derived from precursors present in Beringia by Riss time. The existence of the brown lemming, *Lemmus sibiricus* Kerr, on St. George Island, about 48 km to the north of St. Paul, indicates that the now-submerged areas surrounding the islands were lowlands that supported wet tundra during the Würm period, by which time *S. pribilofensis* probably inhabited the St. Paul highland. The precursor of *S. pribilofensis* was perhaps synchronously present in Beringia with the precursor(s) of the three Recent species of shrews of subgenus *Otisorex* in northeastern Eurasia (*Sorex leucogaster*, *S. portenkoi*, and *S. camtschaticus*). Yudin (1989) suggested that *S. camtschaticus* may represent a shrew that made its way to Eurasia via the Aleutian Islands, Komandorskie Islands, and Kamchatka. Since no indigenous terrestrial mammals are now present in the Aleutian Islands west of Umnak Island, and since the islands were ice-covered during glacial periods (Hopkins 1972), that the northern vole and the varying lemming occurring on Unalaska Island and Umnak Island spread westward from the Alaska Peninsula during early postglacial time seems a tenable consideration. Much evidence indicates that the shrew designated *S. hydrodromus* was collected somewhere within the Unalaska District other than on St. Paul or Unalaska Islands. The data support the conclusion that *S. pribilofensis* is specifically distinct from the shrew that was described as *S. hydrodromus*.

Acknowledgements

The cooperation and generous support of several individuals and organizations made this investigation possible. Dr. Thomas R. Loughlin, National Marine Mammal Laboratory, National Marine Fisheries Service, NOAA, Seattle, approved our use of the Laboratory's facilities on St. Paul Island; there, Mr. Jason Baker and Mr. Bruce Robson, also of that Laboratory, provided much assistance. Mayor John R. Merculief, City of St. Paul, and Mr. Ron Philemonoff, Chief Executive Officer of the Tanadgusix Corporation, Anchorage, permitted us to undertake field work on the Island. Dr. Arthur L. Sowls, Alaska Maritime National Wildlife Refuge, U. S. Fish and Wildlife Service, Homer, Alaska, provided biological data concerning the Pribilof Islands and kindly assisted in many other ways. Ms. Debbie Bordukofsky, St. Paul, provided information about Aleut names for mammals. We express our sincere thanks for these contributions.

Zusammenfassung

Hinweise auf die artliche Selbständigkeit der Spitzmaus (Mammalia: Soricidae) von der Insel St. Paul (Pribilof Inseln, Beringmeer)

Die Chromosomen von einer auf der Insel St. Paul (Pribilof Inseln) vorkommenden Spitzmausart wurden untersucht. Bei einem männlichen Tier bestand der Karyotyp (2 n = 55) aus 52 Autosomen, den

Geschlechtschromosomen (X und Y), und einem sehr kleinen Chromosom ohne Homologon. Die NFa, ausschließlich dem kleinsten Chromosom, war 62. Zwei Namen, *Sorex hydrodromus* Dobson, 1889 und *S.* (*Otisorex*) *pribilofensis* Merriam, 1895, sind in der Vergangenheit auf diese Spitzmaus verwendet worden. Wie in dieser Arbeit besprochen, weisen die Zähne deutliche Unterschiede auf, die eine artliche Trennung der zwei Taxa begründen. Für die auf der Insel St. Paul vorkommende Spitzmaus verwenden wir den Namen *S. pribilofensis*; die richtige spezifische Bezeichnung für *S. hydrodromus* ist unbekannt. Der Karyotyp bzw. andere Artmerkmale unterscheiden *S. pribilofensis* von den drei Vertretern der Untergattung *Otisorex* in Eurasien, gleichfalls von den nearktischen Arten dieser Untergattung. Die meisten Säugetiere, die Inseln im Beringmeer bewohnen, sind Vertreter (Unterarten) von Säugetieren, die auf dem Festland (Eurasien und Nord-Amerika) weit verbreitet sind. *S. pribilofensis* und ein Halsbandlemming (*Dicrostonyx*) sind aber selbständige Arten, die anscheinend vor der letzten pleistozänen Kaltzeit (Würm) die heutigen Inseln schon besiedelt hatten.

References

Corbet, G. B.; Hill, J. E. (1980): A world list of mammalian species. London: British Museum (Natural History).

Dall, W. H. (1870): Alaska and its resources. Boston: Lee and Shepard.

Dobson, G. E. (1889): Description of a new species of water-shrew from Unalaska Island. Ann. and Magazine Nat. Hist. **4**, 372–374.

Dolgov, V. A.; Luk'ianova, I. V. (1966): O stroenii genitalii palearkticheskikh burozubok (*Sorex*, Insectivora) kak systematicheskom priznake. Zool. Zhur. **45**, 1852–1861.

Golovin, P. N. (1862): Obzor Russkikh kolonii v Severnoi Ameriki. [Transl. by B. Dmytryshyn and E. A. P. Crownhart-Vaughan. 1979.] Portland: Oregon Historical Society.

Gureev, A. A. (1979): Nasekomoiadnye (Mammalia, Insectivora). Fauna SSSR, Mlekopitaiushchie Tom **4**, vyp. 2. Leningrad: Nauka.

Hall, E. R. (1981): The mammals of North America. Sec. ed. Vol. 1. New York: John Wiley and Sons.

Hall, E. R.; Kelson, K. R. (1959): The mammals of North America. Vol. 1. New York: Ronald Press.

Hoffmann, R. S.; Peterson, R. S. (1967): Systematics in zoogeography of *Sorex* in the Bering Strait area. System. Zool. **16**, 127–136.

Honacki, J. H.; Kinman, K. E.; Koeppel, J. W. (1982): Mammal species of the world. A taxonomic and geographic reference. Lawrence, Kansas: Allen Press.

Hopkins, D. M. (1972): The paleogeography and climatic history of Beringia during late Cenozoic time. Inter-Nord **12**, 121–150.

Hopkins, D. M. (1973): Sea level history in Beringia during the past 250,000 years. Quaternary Res. **3**, 520–540.

Hopkins, D. M.; Einarsson, T. (1966): Pleistocene glaciation on St. George, Pribilof Islands. Science **152**, 343–345.

Hutterer, R. (1993): Order Insectivora. In: Mammal species of the world. A taxonomic and geographic reference. Ed. by D. E. Wilson and D. A. M. Reeder. Washington: Smithsonian Institution Press. Pp. 60–130.

Ivanitskaia, E. Iu.; Kozlovskii, A. I. (1985): Kariotipy palearkticheskikh zemleroek-burozubok podroda *Otisorex* c kommentariiami po sistematike i filogenii gruppy "*cinereus*". Zool. Zhur. **64**, 950–953.

Jackson, H. H. T. (1928): A taxonomic review of the American long-tailed shrews (genera *Sorex* and *Microsorex*). North American Fauna No. 51. Washington: U. S. Government Printing Office.

Junge, J. A.; Hoffmann, R. S. (1981): An annotated key to the long-tailed shrews (genus *Sorex*) of the United States and Canada, with notes on Middle American *Sorex*. Mus. Nat. Hist., Occas. Papers No. 94. Lawrence: Museum Nat. History, Univ. Kansas.

Levan, A.; Fredga, K.; Sandberg, A. A. (1964): Nomenclature for centromeric position on chromosomes. Hereditas **52**, 200–220.

Matthey, R. (1945): L'évolution de la formule chromosomiale chez les vertébrés. Experientia **1**, 50–60, 78–86.

Merriam, C. H. (1895): Synopsis of the American shrews of the genus *Sorex*. North American Fauna No. **10**. Washington: U. S. Government Printing Office.

Murie, O. J. (1959): Fauna of the Aleutian Islands and Alaska Peninsula. Washington: U. S. Government Printing Office.

Pavlinov, I. Ia.; Rossolimo, O. L. (1987): Systematika mlekopitaiushchikh SSSR. Moskva: Moskovskii Universitet.

Peterson, R. S. (1967): The land mammals of Unalaska Island: present status and zoogeography. J. Mammalogy **48**, 119–129.

Rausch, R. L.; Rausch, V. R. (1995): The taxonomic status of the shrew of St. Lawrence Island, Bering Sea (Mammalia: Soricidae). Proc. Biol. Soc. Washington **108**, 717–728.

Seabright, M. (1972): The use of proteolytic enzymes for the mapping of structural rearrangements in the chromosomes of man. Chromosoma **36**, 204–210.

Sumner, A. T. (1972): A simple technique for demonstrating centromeric heterochromatin. Exper. Cell Res. **75**, 304–306.

Yudin, B. S. (1969): Novye dannye po systematike nekotorykh vidov zemleroek (Soricidae) Palearktiki i Nearktiki. Acta Theriol. **14**, 21–34.

Yudin, B. S. (1972): K systematike transarkticheskoi burozubki (*Sorex cinereus* Kerr, 1792) fauny SSSR. Teriologiia **1**, 45–50.

Yudin, B. S. (1973): K kharakteristike transarkticheskoi burozubki (*Sorex cinereus* Kerr, 1792) severo-vostoka Sibiri i Kamchatki. In: Fauna Sibiri. Trudy Biol. Inst., vyp. 16. Ed. by B. S. Yudin. Novosibirsk: Nauka. Pp. 269–279.

Yudin, B. S. (1989): Nasekomoiadnye mlekopitaiushchie Sibiri. In: Posthumous Volume, Ed. by V. N. Bol'shakov. Novosibirsk: Nauka. Pp. 1–360.

Zyll de Jong, C. G. van (1982): Relationships of amphiberingian shrews of the *Sorex cinereus* group. Canad. J. Zool. **60**, 1580–1587.

Zyll de Jong, C. G. van (1991): Speciation in the *Sorex cinereus* group. In: The biology of the Soricidae. Ed. by J. S. Findley and T. L. Yates. Museum of Southwestern Biol., Spec. Publ. No. 1. Albuquerque: Univ. New Mexico Printing Services. Pp. 65–73.

Authors' addresses: Robert L. Rausch, Department of Comparative, Medicine School of Medicine, Box 35 71 90, University of Washington and Virginia R. Rausch, Mammals Section, Burke Memorial Museum, Box 35 30 10, University of Washington, Seattle, Washington 98195, U. S. A.

Z. Säugetierkunde **62** (1997) 203–208

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The influence of body weight on the quantity of food ingested in *Pipistrellus kuhlii* (Kuhl, 1817) and *Pipistrellus savii* (Bonaparte, 1837) (Chiroptera: Vespertilionidae)

By S. Vergari and Gianna Dondini

Museo di Storia Naturale dell'Università di Firenze, Firenze, Italia

Receipt of Ms. 08. 07. 1996
Acceptance of Ms. 19. 02. 1997

Abstract

The variation in body weight during the summer was monitored in three non-pregnant females of *Pipistrellus kuhlii* and in two non-pregnant females and one male of *Pipistrellus savii*, analysing the influence of this parameter on the quantity of food ingested. The daily percentage increase in body weight of the two species was between 3.5% and 5.1%; the daily percentage decrease in body weight between 3.9% and 5%. There was a significant negative correlation between body weight prior to evening flight and the quantity of food ingested in both species, suggesting a mechanism of negative feedback that permits each specimen to maintain a body weight congruous to the metabolic and mechanical requests imposed by flight, maximising manoeuvrability and minimising both the amount of energy required and risk of predation.

Introduction

The energy cost of flight is very high and, as several authors have demonstrated, increases with body weight (Norberg 1987; Rayner et al. 1989). The metabolic requests of flight have been compared in species of different weights (Carpenter 1985, 1986; Thomas 1975, 1987; Thomas and Suthers 1972) without going into any detail on the influence of individual variation in body weight on the metabolism and physiology of flight (Rayner et al. 1989; Webb et al. 1992). A 5–10% increase in the total weight of a single individual can increase the mechanical potency required for flight by 15% (Rayner et al. 1989). An increase in body weight causes an increase in the wing loading and a consequent worsening of flight performance (Hughes and Rayner 1991). Furthemore, manoeuvrability – defined as the minimum radius of curvature that the animal can obtain in flight – is increased by a low body mass and low wing loading (Thollesson and Norberg 1991).

Bats show two types of variation in body weight during their active periods: 1) daily oscillations (Studier et al. 1970; Studier and Ewing 1971) and 2) long-term variations linked to pregnancy or hibernation (Ewing et al. 1970; Beasley et al. 1984; Speakman and Racey 1987).

An examination of body weight just prior to evening flight is particularly interesting due to the direct influence of weight on both flight and feeding capacity; it also probably influences the bat's ability to flee predators (Ransome 1990). This study presents the results of research conducted on the relationship of body weight before evening flight to quantity of food ingested in two species of male and non-pregnant female bats, *Pipistrellus kuhlii* (Kuhl, 1817) and *Pipistrellus savii* (Bonaparte, 1837).

Material and methods

Early in June 1993 three non-pregnant female Kuhl's bats and a male and two non-pregnant female Savi's bats were captured in the plains of Florence. Both species are insectivorous and are frequently observed flying in urban areas (Lanza 1959).

The animals were kept and tested in a room measuring 3×3×3 m where they had complete freedom of flight, under a natural photo period. Shelters attached to the walls offered the bats refuge during the day. The specimens were kept for about 50 days and then released. During captivity they were fed on mealworms (*Tenebrio molitor*) raised on a regularly renewed substratum composed of bran, proteinic chick food, vegetables and fruit (Wilson 1988; Dondini and Vergari 1995) to which small quantities of mineral salts and powdered calcium were added. Hydrosoluble polyvitamins were added to their drinking water.

After a week of acclimatisation the body weight of each specimen was recorded before and immediately after eating but prior to being given water. Each specimen was weighed on an electronic scale with a 0.1 g degree of precision (Tanita Model 1479). The subjects were fed from 19:30–20:00 (daylight time) – which is about the same time that the bats in the open from the same localities began to hunt – by placing a container full of mealworms inside the room. The bats had unlimited access to the container and ate until satiated.

The quantity of food ingested was calculated by the difference in body weight before and after each meal. The mean weight was calculated by adding the daily weights before feeding and dividing the sum by the days of testing (Wm = W1 + ... Wn/n); the daily percentage weight increase was obtained by dividing the mean daily increase (Wi) by the mean weight (Wi% = [Wi/Wm]*100); the percentage daily weight decrease was obtained by dividing the mean decrease (Wd) by the mean weight (Wd% = [Wd/Wm]*100). Regression analysis was made on the ratio between the weight of each specimen prior to feeding and the quantity of food ingested.

Results and discussion

In *P. kuhlii* and *P. savii* individual weight oscillates more or less regularly (Figs. 1, 2). Both species show a daily percentage increase between 3.5% and 5.1% of their mean weight and a daily decrease between 3.9% and 5.1% (Tab. 1).

Regression analysis reveals a significant inverse correlation between body weight prior to flight and quantity of food ingested in both *P. kuhlii* (P.k. 1: $r = -0.500$, $P < 0.01$, $n = 40$; P.k. 2: $r = -0.435$, $P < 0.01$, $n = 40$; P.k. 3: $r = -0.428$, $P < 0.01$, $n = 40$) and *P. savii* (P.s. 1:

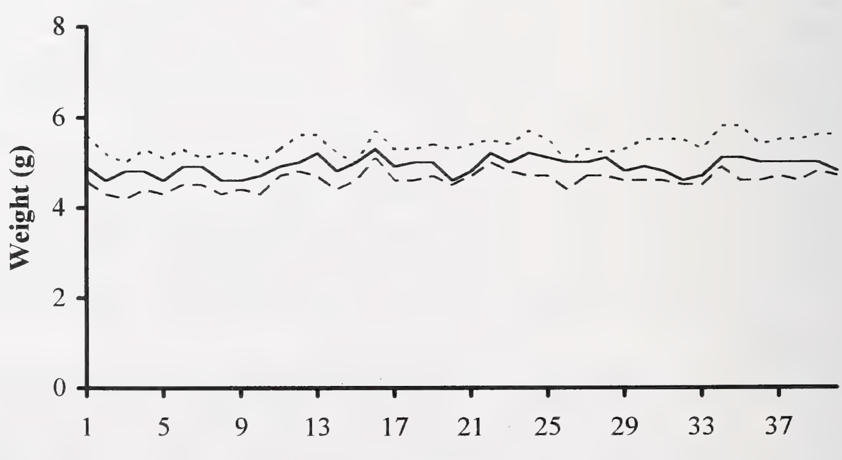


Fig. 1. Variation of body weight in *Pipistrellus kuhlii* over 40 days. — = *P.k.* 1; - - - = *P.k.* 2; .··· = *P.k.* 3.

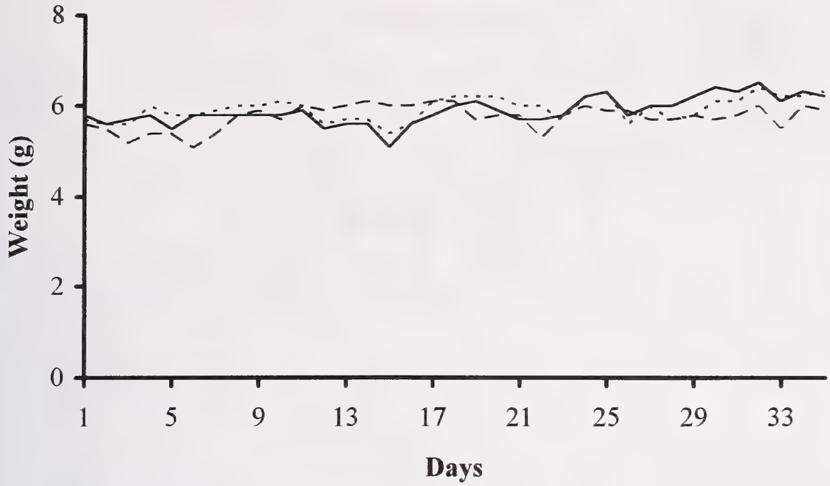


Fig. 2. Variation of body weight in *Pipistrellus savii* over 35 days. ... = *P. s.* 1; - - - = *P.s.* 2; — = *P.s.* 3.

Table 1. Wm = mean weight; Wmin = minimum absolute weight; Wmax = maximum absolute weight; Wi = mean daily increase; Wi% = daily percentage weight increase; Wd = mean daily decrease; Wd% = daily percentage weight decrease. *P.k.* = *P. kuhlii*; *P.s.* = *P. savii*.

	P.k. 1	*P.k.* 2	*P.k.* 3	*P.s.* 1	*P.s.* 2	*P.s.* 3
Sex	F	F	F	M	F	F
Forearm (mm)	29.3	30	31.7	32	33	34.1
Wm (g)	4.6	4.7	5.3	5.6	5.9	5.9
Wmin (g)	4.2	4.1	5	5.1	5.3	5.4
Wmax (g)	5	5.1	5.8	6.3	6.4	6.4
Wi (g) (±SE)	0.23 (±0.034)	0.20 (±0.026)	0.24 (±0.043)	0.19 (±0.028)	0.23 (±0.037)	0.23 (±0.043)
Wi%	5.1%	4.2%	4.5%	3.4%	3.9%	4%
Wd (g) (±SE)	0.19 (±0.028)	0.23 (±0.031)	0.25 (±0.034)	0.29 (±0.038)	0.23 (±0.04)	0.28 (±0.055)
Wd%	4.1%	5%	4.8%	5.1%	3.9%	4.7%
Days	40	40	40	35	35	35

$r = -0.711$, $P < 0.01$, $n = 35$; P.s. 2: $r = -0.499$, $P < 0.01$, $n = 35$; P.s. 3: $r = -0.599$, $P < 0.01$, $n = 35$). In both species an increase in body weight negatively influences the quantity of food ingested (Figs. 3, 4). A statistical analysis of the regressions showed no significant differences between the inclination of the straight lines in either species.

An analysis of body weight has shown that this oscillates in time. Nursing females of *Plecotus auritus* show a daily decrease in body weight which is significantly and positively correlated to the minimum temperature of the preceding night (Speakman and Racey 1987). During the period in which the present observations were conducted the thermal excursion was limited and the minimum temperature was always between 17 and 19 °C, which allows us to exclude any appreciable influence of temperature on body weight during testing. This result tends to confirm the observation by Aldridge and Brigham (1988) that a radio transmitter applied to a bat begins to have a notably negative influence on the animal's flight ability when the instrument surpasses 5% of its body weight. Body weight influences manoeuvrability and the alteration of this parameter can increase the risk of capture by nocturnal predatory birds or accidents (Gillette and Kimbrough 1970; Krzanowski 1973; Ruprecht 1979; Perez-Barberia 1991; Speakman 1991; Scaravelli and Aloise 1993).

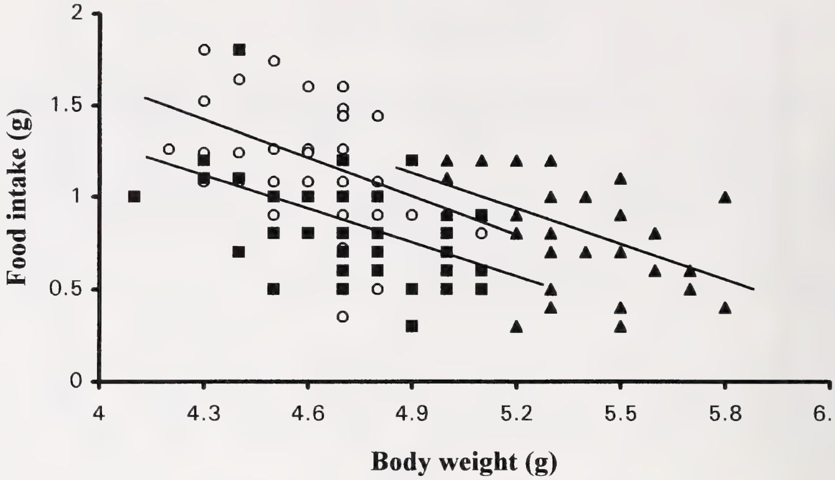


Fig. 3. Regression analysis between body weight (abscissa) and food ingested (ordinate) in 3 specimens of *Pipistrellus kuhlii*. ○ = *P.k.* 1 (y = –0.51x + 6.02, r = –0.500); ■ = *P.k.* 2 (y = –0.258x + 3.2, r = –0.435); ▲ = *P.k.* 3 (y = –0.25x + 3.5, r = –0.428).

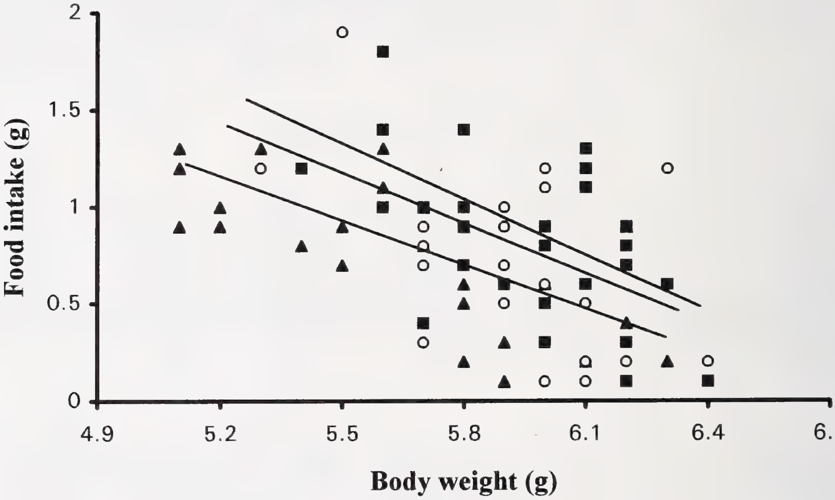


Fig. 4. Regression analysis between body weight (abscissa) and food ingested (ordinate) in 3 specimens of *Pipistrellus savii*. ▲ = *P.s.* 1 (y = –0.36x + 4.8, r = –0.711); ○ = *P.s.* 2 (y = –0.44x + 5.98, r = –0.499); ■ = *P.s.* 3 (y = –4.9x + 6.68, r = –0.599).

Thus, bats probably maintain their body weight within strict limits so as not to compromise their flight ability. Prior to hibernation and in pregnant females, when an increase in weight is inevitable, the negative consequences are apparently overcome by muscular modifications which allow the animals to adapt to the increased load (Rayner et al. 1989).

It can thus be hypothesized that males and non-pregnant females are subject to a process of negative feedback between the quantity of food ingested and body weight, which maintains the latter within limits compatible with the mechanical and metabolic requests of flight. Such a limit maximises manoeuvrability and minimises both the energy cost and risk of predation.

Acknowledgements

We are most grateful to Dr. Ulla Norberg (Department of Zoology, University of Göteborg), Prof. Benedetto Lanza, and Prof. Francesco Dessì-Fulgheri, both of the Department of Biology and Genetic, University of Florence, for their helpful suggestions on the manuscript.

Zusammenfassung

Der Einfluß des Körpergewichts auf die Menge der aufgenommenen Nahrung bei Pipistrellus kuhlii (Kuhl, 1817) und Pipistrellus savii (Bonaparte, 1837) (Chiroptera: Vespertilionidae).

Die Veränderung des Körpergewichts während des Sommers wurde an drei Exemplaren (nicht trächtigen) von weiblichen *P. kuhlii*, sowie an zwei (nicht trächtigen) weiblichen und einem männlichen *P. savii* in Beziehung zur Nahrungsmenge untersucht. Die tägliche Zunahme des Körpergewichts beider Arten lag zwischen 3,5% und 5,1%; die tägliche Abnahme an Körpergewicht zwischen 3,9% und 5%. Es besteht bei beiden Arten eine signifikante negative Relation zwischen dem Körpergewicht vor dem Nachtflug und der Menge der aufgenommenen Nahrung. Das legt eine negative Rückkoppelung nahe, die jedem Exemplar erlaubt, ein Körpergewicht beizubehalten, das den Anforderungen des Fliegens hinsichtlich Stoffwechsel und Mechanik entspricht. Die Manövrierfähigkeit wird maximiert und der Betrag der benötigten Energie wie auch das Risiko, selbst erbeutet zu werden, werden minimiert.

References

Aldridge, H. D. J. N.; Brigham, R. M. (1988): Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. J. Mammalogy **69**, 379–382.

Beasley, L. J.; Pelz, K. M.; Zucker, I. (1984): Circannual rhythms of body weight in pallid bats. Am. J. Physiol. **246**, R955–R958.

Carpenter, R. E. (1985): Flight physiology of flying foxes, *Pteropus poliocephalus*. J. exp. Biol. **114**, 619–647.

Carpenter, R. E. (1986): Flight physiology of intermediate sized fruit bats (family Pteropodidae). J. exp. Biol. **120**, 79–103.

Dondini, G.; Vergari, S. (1995): Rearing and first reproduction of the Savi's pipistrelle (*Pipistrellus savii*) at Group of Study and Conservation Chiroptera, Florence. Int. Zoo Yb. **35**, 143–146.

Ewing, W. G.; Studier, E. H.; O'Farrell, M. J. (1970): Autumn fat deposition and gross body composition in three species of *Myotis*. Comp. Biochem. Physiol. **36**, 119–129.

Gillette, D. D.; Kimbrough, J. D. (1970): Chiropteran mortality. In: About bats. Ed. by B. H. Slaughter and D. W. Walton. Dallas: Southern Methodist Univ. Press. Pp. 262–283.

Hughes, P. M.; Rayner, J. M. V. (1991): Addition of artificial loads to Long-Eared bats *Plecotus auritus*: handicapping flight performance. J. exp. Biol. **161**, 285–298.

Krzanowski, A. (1973): Numerical comparison of Vespertilionidae and Rhinolophidae (Chiroptera: Mammalia) in the owl pellets. Acta zool. Crac. **18**, 133–140.

Lanza, B. (1959). Chiroptera. In: Fauna d'Italia Vol. IV, Mammalia, generalità, Insectivora, Chiroptera. Ed. by A. Toschi and B. Lanza. Bologna: Edizioni Calderini. Pp. 187–473.

Norberg, U. M. (1987): Wing form and flight mode in bats. In: Recent advances in the study of bats. Ed. by M. B. Fenton, P. A. Racey, and J. M. V. Rayner. Cambridge: Cambridge Univ. Press. Pp. 43–56.

Perez-Barberia, F. J. (1991): Influencia de la variacion latitudinal en la contribucion de los murciélagos (Chiroptera) a la dieta de la Lechuza comun (*Tyto alba*). Ardeola **38**, 61–68.

Rayner, J. M. V.; Jones, G.; Hughes, P. M. (1989): Load carrying by flight bats. In: European Bat Research 1987. Ed. by V. Hanàk, I. Horàcek, and J. Gaisler. Praha: Charles Univ. Press. Pp. 235–245.

Ransome, R. (1990): The natural history of hibernating bats. London: Christopher Helm.

Ruprecht, A. L. (1979): Bats (Chiroptera) as constituents of the food of barn owl *Tyto alba* in Poland. Ibis **121**, 489–494.

Scaravelli, D.; Aloise, G. (1993): Predazione da rapaci su Chirotteri in Italia. Suppl. Ric. Biol. Selvaggina **21**, 529–534.

SPEAKMAN, J. R. (1991): The impact of predation by birds on bat population in the British Isles. Mammal Rev. **21**, 123–142.

SPEAKMAN, J. R.; RACEY, P. A. (1987): The energetics of pregnancy and lactation in the brown long-eared bat, *Plecotus auritus.* In: Recent advances in the study of bats. Ed. by M. B. FENTON, P. A. RACEY, and J. M. V. RAYNER. Cambridge: Cambridge Univ. Press. Pp. 367–393.

STUDIER, E. H.; EWING, W. G. (1971): Diurnal fluctuation in weight and blood composition in *Myotis nigricans* and *Myotis lucifugus.* Comp. Biochem. Physiol. **38**, 129–139.

STUDIER, H. E.; PROCTER, J. W.; HOWELL, D. J. (1970): Diurnal body weight loss and tolerance of weight loss in five species of *Myotis.* J. Mammalogy **51**, 302–309.

THOLLESSON, M.; NORBERG, U. M. (1991): Moments of inertia of bat wings and body. J. exp. Biol. **158**, 19–35.

THOMAS, P. S. (1975): Metabolism during flight in two species of bats, *Phyllostomus hastatus* and *Pteropus gouldii*. J. exp. Biol. **63**, 273–293.

THOMAS, P. S. (1987): The physiology of bat flight. In: Recent advances in the study of bats. Ed. by M. B. FENTON, P. A. RACEY, and J. M. V. RAYNER. Cambridge: Cambridge Univ. Press. Pp. 75–99.

THOMAS, P. S.; SUTHERS, R. A. (1972): The physiology and energetics of bat flight. J. exp. Biol. **57**, 317–335.

WEBB, P. I.; SPEAKMAN, J. R.; RACEY, P. A. (1992): Inter- and intra-individual variation in wing loading and body mass in female pipistrelle bats: theoretical implication for flight performance. J. Zool. (London) **228**, 669–673.

WILSON, D. E. (1988): Maintaining bats for captive studies. In: Ecological and behavioral methods for the study of bats. Ed. by T. H. KUNZ. Washington D. C.: Smithsonian Institution. Pp. 247–264.

Authors' address: SIMONE VERGARI and GIANNA DONDINI, Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia "La Specola", Via Romana 17, I-50125 Firenze, Italia.

Z. Säugetierkunde **62** (1997) 209–218

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

The implications of territoriality for the social system of the European pine marten *Martes martes* (L., 1758)

By R. Schröpfer, P. Wiegand, and H.-H. Hogrefe

Department of Biology/Chemistry: Ethology, University of Osnabrück, Osnabrück, Germany

Receipt of Ms. 12. 01. 1996
Acceptance of Ms. 12. 02. 1997

Abstract

The social organisation and the structure of a population of pine martens in the northern part of a low mountain range in northwestern Germany are investigated in a long-term study. Observations by radio-tracking and data from capture-recapture of 12 pine martens (6 females, 6 males) show at least four differences in territory size: the seasonal, the intersexual, that due to the mating system, and that due to genesis.

The territories are held over several years. Males already create summer territories in early spring, before the birth of the offspring and about 5 months before the mating season. They leave these only in late autumn and move into their winter territories. This extensive seasonal territorial behaviour cannot only be explained as mate guarding, but also as offspring guarding by creating a territory-tie. Genetic paternity could be determined by the DNA-fingerprinting method. Parental care of the young by the territorial male was never observed. But males show a distinct guarding behaviour by creating a territorial tie. This social structure is called a male-mother-family.

Introduction

As a number of related Mustelidae species, the pine marten possesses a delayed implantation (Aubert and Canivenc 1986), so that the mating season and the birth of the young lie about 8 months apart. The question is how the male manages to assure his reproductive success in both seasons.

Pine martens are stenotopic silvicolous carnivores, lead a solitary life and occupy intrasexual territories. A male territory can overlap the territory of one or more females (Schröpfer et al. 1989).

In fact, a solitary life seems to be in opposition to a social organisation of both sexes and consequently also to social organisation. Such questions were mainly dealt with in ornithological observations and discussions (Davies 1991). Observations of mammals can hardly be found (Clutton-Brock 1991; Clutton-Brock and Harvey 1978).

For this investigation, it is supposed that the specific territorial behaviour creates an intersexual territory-tie and a specific social organisation that assures the fitness of both sexes.

Material and methods

Study area

The observation area is a forest region, Osnabrücker-Hügelland, lying in the western part of the low mountain range on the southern border of the lowland plain of northwestern Germany. With heights from 85 m to 163 m above sea-level, it belongs to an area of the planar to hilly level. In this region with

a moderate sub-oceanic climate, there is a yearly rainfall of about 800–850 mm; the average humidity is 82% and the fluctuation in yearly temperature is 16.3 °C on average, while the mean temperature in January is 1.0 °C and in July 16.9 °C.

Only a small part of this area is covered by potentially natural vegetation, such as mixed forests of red-beech and oaks (*Fago-Quercetum*), a forest of oaks and birches (*Betula-Quercetum*) or a forest of alders and ashes (*Fraxino-Alnetum*), forming together 16.4%. The proportionately largest area is now formed by spruce forests (*Picea abies*) with 69%, by a cultivated area of larches (*Larix decidua*) 7.5%, by pine forests (*Pinus sylvestris*) 6.6% and by Douglas spruces (*Pseudotsuga menziesii*) 0.5%. According to Palsterkamp Forestry Office records, it can generally be stated that almost 50% of the whole area consists of spruce trees up to forty years of age 45% up to eighty years and 5% over eighty years of age.

The shape of the forest resembles an extended rectangle, from east to west extending about 10 km and from north to south about 2.5 km. In the north, there are some isolated forest islands where pine martens also occur.

Individuals and methods

In this long-term project, pine martens have been caught in live traps (single door boxes constructed in the Dept. of Biology) since the summer of 1987 during operations carried out over several days or weeks.

Constitution, reproductive stage (the size of the praeputial gland field, of the testes and of the nippels) and determination of the age (the weight and the condition of the teeth) were thoroughly tested each time. Each individual was marked with an ID-chip (EuroID, Weilerswist, Germany) for later recognition and for radio-tracking it received a collar-transmitter (motion detector, 150.150 MHz, Karl Wagener-Senderbau, Cologne, Germany) representing about 2% of body weight. The receivers were built in the electronics workshop of the University's Department of Biology/Chemistry. Several 12-channel pocket-receivers with portable antennae (HB 9 CV) and 2 receivers installed on cars were employed. When the animals were in hollows, they could only be tracked from a distance of a few metres. In tree-tops, their most frequent resting places, they could be tracked from a maximal distance of 5 km.

In capture-recapture operations of the 12 animals (6 males, 6 females) some could only be caught once (6 animals) others twice and more often (6 animals; partly up to 11 times). Most pine martens were observed over a few months, or over a few years, and one female almost continually over a 9 year period.

Direct observation of the animals was seldom possible. Therefore, the observational method consisted of two procedures: 1) the animals were located by means of the receiver signal, and their resting place was mapped; or 2) the animals were tracked at certain intervals throughout the night in order to determine their activities and to track the distance they covered. Their day resting sites were mapped noting the tree in which the marten was sleeping. Because of the shape of the forest region, the distance of the located animals was only about 100 m, therefore the tracking location could be noted up to within a few square metres. Tracking and habitat maps were established for each pine marten, which was possible even when it was caught only once. The mapped data and the observational data were recorded and analysed with the McPaal 2.0 programme (Smithsonian Institution, 1988). In addition to the observation points, the forest bounds and other structures of the study area were recorded, when thought to be helpful. By means of the programme, the area sizes (Minimum Convex Polygon MCP) were calculated. It must be stressed that only the locations of day resting sites, and not the locations of tracking observations at night, were included in the calculation of the territory sizes. A track unit was the distance covered by an individual in one night, measured when leaving the resting place in the evening until taking up the same or another resting place the morning thereafter. This method was used in summer as well as in winter. The observation series could cover one to eight nights. The latter was intended to give information about how intensively the martens roam the area in successive activity phases.

Furthermore, pine martens captured by hunters in northwestern Germany were measured for a constitutional analysis. Data were gained from these animals which cannot be obtained from live catches, especially for the determination of age and the reproduction analysis. As the pine martens from the observation area do not differ in size from other individuals of northwestern Germany (t-test = 0.238, df = 86, p = 0.81), the more representative sample was used for the representation of proportions of body sizes.

The determination of paternity was performed with the DNA fingerprinting method. Tissue material used for DNA extraction included bone fragments (Wiegand et al. 1992) from the feet (metatarsalia)

of the dead animals and blood from the tail vein of the pine martens caught alive. The extracted DNA was quantified fluorimetrically (Bontemps et al. 1975). The degree of DNA degradation was investigated using 1.0% agarose gels with subsequent ethidium bromide staining (Sambrook et al. 1982). After digestion (restriction enzyme: Hinf I) the DNA was transferred by Southern-blotting onto a nylon membrane (Hybond N, Amersham, UK) according to Brinkmann et al. (1991). Probe hybridisation was carried out using the radioactive labelled multi locus probe MZ 1.3 (Biotest, Germany). MZ 1.3 was isolated from a human genomic library which had been constructed from DNA partially digested with Sau 3 A. The repeat structure showed a 27 bp repeat unit which was approximately 40 times repeated (Schacker et al. 1990).

Autoradiographs of different exposure times were prepared from each blot, because the loading of equimolar DNA concentrations in each lane was not possible, due to varying extraction amounts depending on the tissues used. Two commercially available DNA size standards were used: DNA Analysis Marker (Promega, USA) and Drigest III lambda phage marker (Pharmacia, Germany).

From the autorads only the bands >3 kb were analysed (Jeffreys et al. 1985). The comparison of band patterns was done manually. A total of 34 different band positions could be determined for all animals by comparing these positions to the band positions of the individual patterns (so-called "present-absent matrix" – Kirby 1990; Gilbert et al. 1990). All individual DNA patterns in this group were compared in pairs, leading to 45 comparisons for 10 animals. For the calculation of the band sharing rate, the formula $2N/a + b$ was used (N = number of corresponding bands between 2 individuals, a + b = number of bands from individual a + b) (Jeffreys et al. 1985).

Additionally, a cluster analysis was carried out (UPGMA-method = unweighed pairs between groups; average linkage analysis) using the present-absent matrix of the individual band patterns (Gilbert et al. 1990).

Results

The observations lead to the supposition that the females and the males behave differently in the arrangement of their territories. The two females that could be observed over the longest period, F1 and F6, reduced their territories during these years: at subadult age (approximately in the second summer) the female F1 occupied a territory that was about 8 times as large as that in her fourth and fifth year. She settled in the western part of the territory which she had previously occupied, after having reduced it constantly ($y = 545.2 - 96.5x$; $r = -0.86$; $p < 0.001$; $n = 6$) (Fig. 1). In this territory of only about 70 ha, the female could be observed during the breeding of 5 litters. The female F6 behaved very similarly:

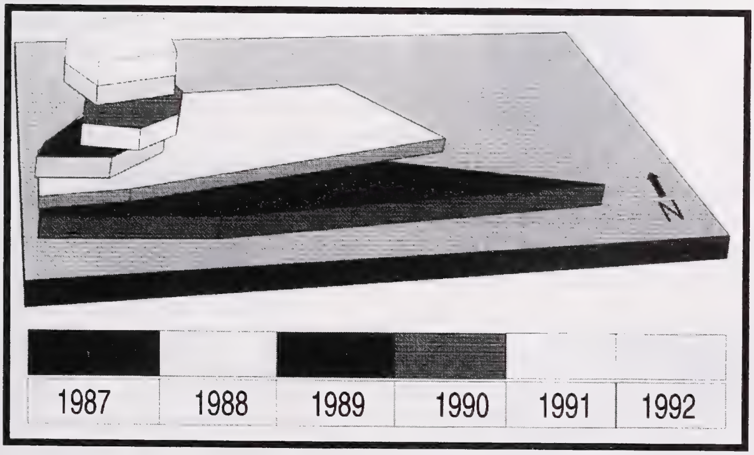


Fig. 1. Changes in size and location of the territories (territory-genesis) of the female F1 over 6 years (Starting at the bottom with the plateau representing the forest area)

she reduced her territory from almost 500 ha to 100 ha from the first winter during the summers until the third winter of observation ($y = 638 - 129.7x$; $r = -0.9$; $p < 0.001$; $n = 4$). It could be shown that she had her first litter in the second summer. At that time she occupied 250 ha. Before F6 settled in this area, the female F2 had lived there for four years followed by F4 which occupied the area for two years; both had their offspring there. The summer territories had similar sizes of 230 ha and 207 ha, respectively. The female F4 could be observed over two summers and two winters. The two summer territories were of the same size (206 ha and 207 ha, respectively); but she transferred her territory totally to the west in the second summer and had her offspring in the territory left by F2. She reduced her territory each winter: the first time to 153 ha and the second time to 58 ha. However, it must be borne in mind that in the first summer the female was subadult. The long-term observations lead to the conclusion that the females in fact only occupied a territory of a size necessary for themselves and the care of their young.

Up to now, only two of the six males could be observed over a longer period. But in their case it could clearly be seen that their summer territories were much larger than the winter territories (Fig. 2). This does not apply to the females (Mann-Whitney-test: $z = -0.05$; $p = 0.9$; $n = 16$). Although the male R1 lived in a closed forest of which the other male R2 occupied only a small part, the rest being composed of some isolated forest islands, they did not differ in their behaviour. The summer territory of R1 included two female territories, the territory of R2 only one. The location and the expanse of one of R1's summer territories with a size of 1,240 ha led to the supposition that it included 3 female territories, although the presence of a third female could not be proven by trapping. The smaller winter territories of the males were situated either between the female winter territories or enclosed an existent female territory. In an intersexual comparison, the males' summer territories are larger than the females' (Mann-Whitney-test: $z = -2.9$; $p = 0.004$; $n = 15$). The same applies to the year-long territories, if the winter territories are also taken into account (Mann-Whitney-test: $z = -3.9$; $p < 0.001$; $n = 26$).

As the female cares for the young during the summer months and the mating season occurs in midsummer, the sizes of the summer territories are especially of interest in terms of reproduction. A comparison on the basis of sexual dimorphism of body size and

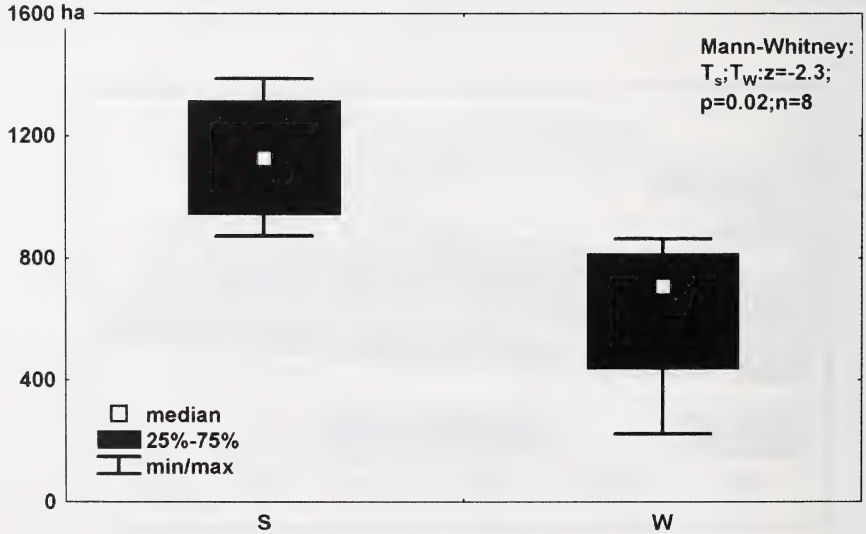


Fig. 2. Size (ha) of the summer and winter territories (T) of the two males R1 and R2 (S: summer, W: winter)

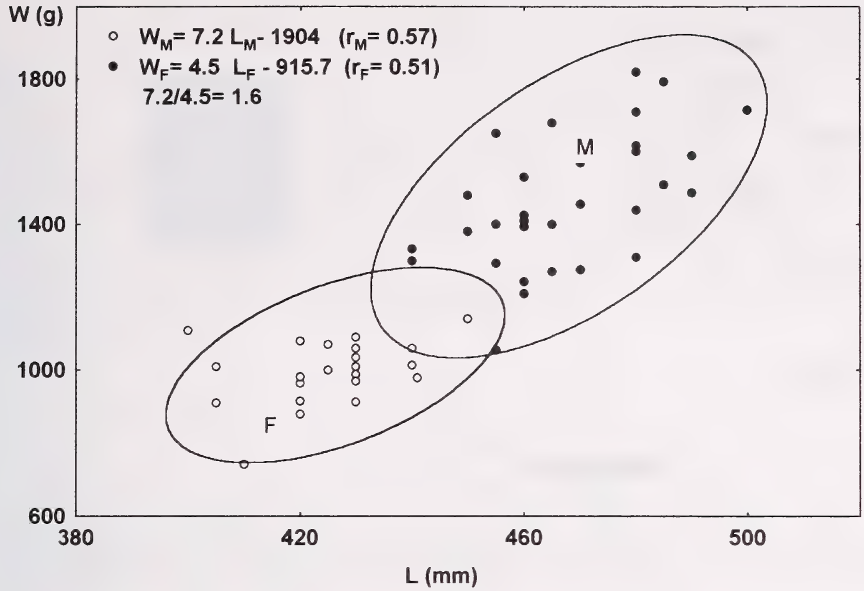


Fig. 3. Size-functions and size-index of the pine marten in northwest Germany (M: male, F: female, W: weight, L: head-body length, 95%-ellipse)

territory size shows that there is no equal proportion between both: the males are 1.6 times larger than the females, according to a function index calculated on body length and body weight (Fig. 3); whereas the male territories are about 4 times as large as the female territories. Consequently, calculated on the basis of 11 female summer territories, a male summer territory should have a nominal size of 257 ha; but the mean size of 4 male summer territories was actually 1,126 ha. This means that in summer the males occupied a proportionally much larger territory than the females.

It should be noted in this context that the size of the male territory was not just the sum of the enclosed female territories. Female territories did not have common boundaries or were arranged irregularly. The male managed to encompass existing, geographically favourable female territories, the result of which was a polyterritoriality.

This difference in female and male behaviour is confirmed by the tracks observed at night. Their respective locations were gained and analysed independently of the locations of day-resting sites. The distances covered by the male R1 during the summer months were much longer than those of the females F1 and F4 (t-test: $t = -8.06$; $df = 54$; $p < 0.001$). The intersexual differences in territory sizes correspond to the differences in the distances covered at night, the ratio of which is 1 : 4.5 in favour of the male. This also corresponds to the fact that the male R1 covered much greater distances in summer than in winter (Fig. 4). It shows the male's great roaming endurance. On average, he covered a distance of 10,808 m during summer nights; the longest track of the male R1 in one night during a mating season was 18,000 m.

As observations in enclosures suggest that a male "on tour" in summer scent-marks certain points, he probably scent-marks his territory during night activity. The question is whether he manages to keep away rival males from his territory by this extensive marking behaviour. As far as reproduction success is concerned, this could be checked by a paternity determination with DNA-fingerprinting for the male R1 with the offspring of each female F1 and F2. The cluster in the dendrogram (Fig. 5) shows that the territorial male R1 was in fact the only eligible male during the mating season for both female territories.

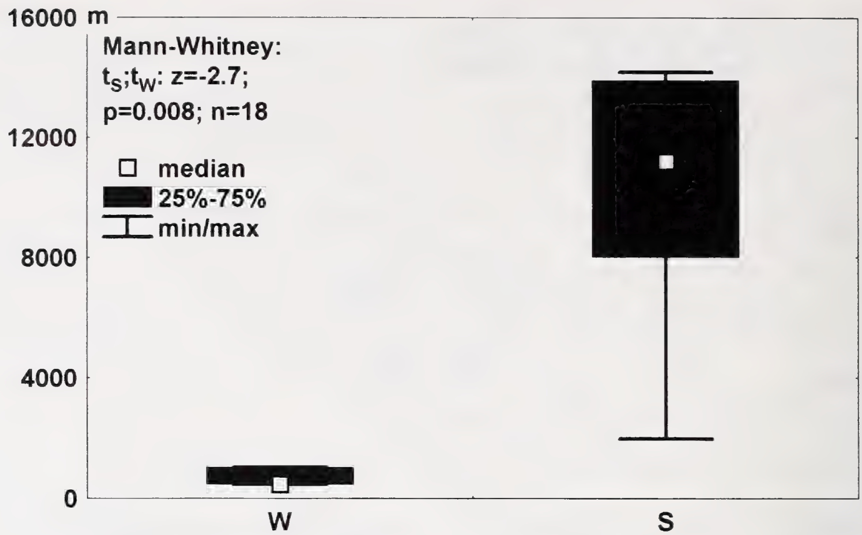
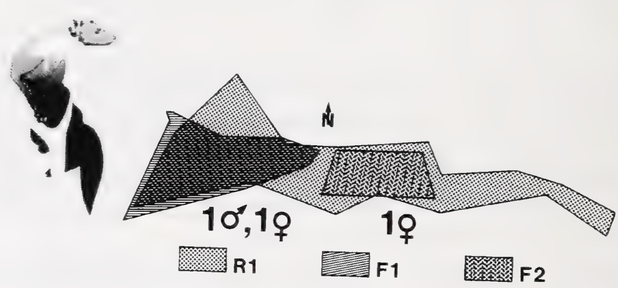


Fig. 4. Length (m) of the winter and summer tracks (t) of the male R1 (S: summer, W: winter)



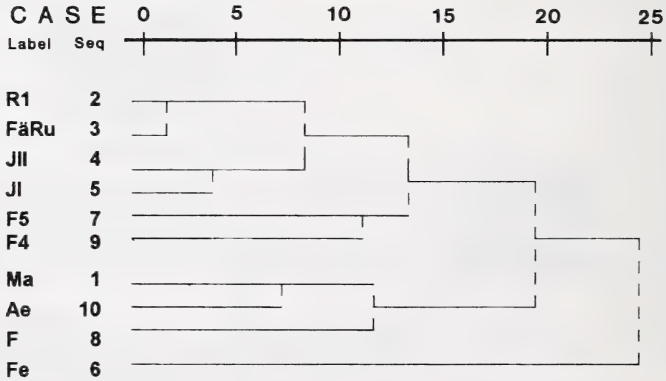


Fig. 5. The paternity of the male R1 with regard to the siblings JI and JII, offspring of the female F1, and the daughter FäRu of the female F2 (MPGMA-method). (Respective territories are illustrated; F4, F5, Ma, Ae, F, Fe: 6 pine martens of other parts of the forest area and of the northwest of Lower Saxony)

This male R1 stayed in the area for 5 years. In the second spring after his disappearance two strong males, about 4 years old, appeared unexpectedly in the area within 2 months (February and March) – R3 (1,745 g) and R4 (1,667 g). R3 could only be observed for 3 days and R4 only for a fortnight. Since that time they have not been trapped again. Instead, a new male R5 (1,517 g), about 3 years old, settled in the western part of the territory previously held by the male R1, where the female F1 lived. A similar occurrence was noted in the territory of R2: after this individual was killed on the road, his territory was taken over by the 3 year-old male R6 (1,637 g).

From the parental analysis and the chronology in which the forest habitat was occupied by the males and the females, it can be deduced that the resident males obviously succeeded in defending their territories intrasexually; but intersexually territories typically overlap for several years.

Discussion

As the study shows, there are at least four differences in territory size: the seasonal, the intersexual, that depending on the mating system and that depending on the genesis.

Thus, the intrasexual territoriality of the pine marten described by Schröpfer et al. (1989) has been confirmed. The territories of adult individuals of the same sex do not overlap, or only partly; and the territories of the males are larger than those of the females.

Direct comparisons of absolute territory sizes given in publications can very rarely be drawn. It is very important to specify the method used for the calculation, as well as the seasons in which the observation was performed. The available data were either collected by means of snow-tracking in winter (Pulliainen 1980, 1982, 1984) or by radio-tracking during other seasons (Clevenger 1993; Krüger 1990; Storch 1988). Data collected over the entire year are rare (Marchesi 1989; Balharry 1993).

Some relations in territory size correspond approximately to those mentioned here. Schröpfer et al. (1989) found that the ratio of female to male territory is 0.33. In this study the proportion is 0.2. Because in most cases the summer territories also determine the maximum area size within one year (Schröpfer et al. 1989), the literature can be consulted for information concerning the territories occupied throughout the year. Marchesi (1989) gives details for the Swiss Jura with a ratio of 0.3 (MCP). Balharry (1993) reports data from two areas of observation in Scotland, won by tracking. According to the medians, a value of 0.3 and 0.6, respectively, was calculated. According to Storch (1988) the values are 0.37 and 0.58, comparing winter to summer territories.

The low value of 0.2 for the female territories in the area of northwestern Germany is not the consequence of larger male territories but can be explained by the observation that the female territories were reduced to a minimum size in the third and fourth summer (minimising of territory size).

The intersexual differences in territory size can also be looked at from the point of view of the hypotheses of basis energy (McNab 1963). Thereupon, Sandell (1989) studied numerous solitary carnivore species. According to Sandell's (1989) calculations the value 2.47 ± 1.06 is in favour of the male territories. The value of 4 found for the observed males lies above the standard division. All this points to the fact that the pine marten male attempts to make its summer territory as large as possible (maximising of territory size). This territory size probably has nothing to do with a higher metabolism, i. e. a greater food availability (see Gittleman and Harvey 1982). Even in the summer in which the male R1 could monopolise only one female, the male covered about 800 ha, even though the female territory was only 70 ha and was situated on the periphery of the male's terri-

tory. In this case the close proximity of a rival male was probably the reason for the large territory size.

Relatively large male territories, therefore, do not contradict the data concerning the small number of females that were found with the male pine martens. As in the literature (Marchesi 1989; Storch 1988; Balharry 1993), and also in the present study, only 1 or 2 female(s) for each male could be counted. It is probable that this did not seldom lead to a monogamous instead of a polygamous (bigamous) mating system. As monogamy here depends on the accessibility of females, it is a facultative monogamy according to Kleiman's (1977) mating categories. This situation relates to the male; for the female, it is always a monogamous relationship (see Wickler and Seibt 1983).

It is remarkable that in the literature only one female is repeatedly allotted to each male territory in the pine marten, although polygyny is common in the Mustelidae (Moors 1980). The forest habitat with its spatial heterogeneity and free spaces, which makes mate guarding more difficult, may have some influence here. As the determination of paternity shows, the male seems to manage mate guarding in the case of 2 females. This can only be understood by citing the intensive marking behaviour of this marten species as an explanation. The existence of preputial gland fields makes this possible (Stubbe 1969; Monte and Roeder 1990a). Observations in enclosures have clearly shown that both sexes, but particularly the male, scent-mark intensively as early as spring (Goethe 1964; Monte and Roeder 1990b, 1993). By means of this territorial marking behaviour of the male, a territorial tie is formed between male, female and offspring.

This assumption is emphasised by the fact that the male already creates the summer territory in early spring, long before the mating season begins (Schröpfer et al. 1989). This period, determined here by tracking, coincides with the increase in testosterone-level in spring, noted by Balharry (1993). That is the reason why the male establishes the summer territory before the birth of its offspring. As our own observations show, the male keeps its summer territory well up to November; only thereafter reducing it. The existence of the summer territory over about 8 months ("pine marten summer") coincides with the very slow development of the young, which are independent only at the beginning of the winter, a characteristic of pine martens and not found in other Mustelidae species (Schmidt 1934, 1943; Heptner and Naumov 1974; own observations).

According to the definition of paternal behaviour, direct care of the offspring is presupposed (i.e. supply with food), but this paternal care cannot be observed in the case of the male pine marten (Schmidt 1943; own observations). Thus, it must be concluded that while the territorial male is the genetic father it is not the parental father, and therefore one cannot speak of a parental family. Nevertheless, the territorial behaviour of the male offers protection for its offspring. Hence, this social system, with reference to Degener's (1918) detailed system of social forms, can be termed a male-mother-family system. This definition appears to deal best with all aspects of care behaviour in this solitary marten species.

Acknowledgements

We would like to thank the following persons for their assistance in this project: W. Biedermann, W. Galisch, G. Schmitz, A. Schwegmann, N. Spreckelmeyer, H. Szczesniak, and R. Tammen. The Institute for Forensic Medicine at the University of Münster, Germany, kindly gave us the means to undertake the DNA fingerprinting analysis. The project is supported by a grant from the State of Lower Saxony.

Zusammenfassung

Die Bedeutung der Territorialität für das Sozialsystem des Europäischen Baummarders Martes martes (L., 1758)

In einer Langzeitstudie werden die soziale Organisation und die Struktur der Population von Baummardern in der nördlichen Mittelgebirgsstufe Nordwestdeutschlands untersucht. Die telemetrischen Beobachtungen und die Fang-Wiederfangdaten von 12 Baummardern (6 Fähen, 6 Rüden) lassen in der Territoriumsgröße einen saisonalen, einen intersexuellen, einen vom Paarungssystem und einen von der Territoriumsgenese abhängigen Flächenunterschied erkennen. Einem Körpergrößen-Unterschied von 1,6 von Fähe und Rüde steht ein Vierfaches der Territoriumsgröße des Rüden gegenüber.

Die Territorien werden über mehrere Jahre besetzt gehalten. Da die Rüden schon im zeitigen Frühjahr vor der Geburt der Jungtiere und ca. 5 Monate vor der Ranzzeit die Territorien einrichten, und diese erst im Spätherbst aufgeben (Baummarder-Sommer), um die Winterterritorien zu beziehen, wird dieses jahreszeitlich ausgedehnte territoriale Verhalten nicht nur als ein Partner-Hüten sondern auch als ein Jungtier-Hüten durch Territorien-Bindung erklärt. Mit DNA-fingerprinting konnte zwar genetisch die Vaterschaft nachgewiesen, eine elterliche Wurfpflege des territorialen Rüden aber niemals beobachtet werden. Da er jedoch das ausgeprägte Hüteverhalten durch territoriale Bindung zeigt, wird diese Sozialstruktur als eine Mann-Mutter-Familie bezeichnet.

References

Aubert, I.; Canivenc, P. (1986): Nidation différée chez les mustélides: Étude ultrastructurale utéro-blastocytaire chez le blaireau européen, la matre et la fouine. Arch. Biol. (Bruxelles) **97**, 157–186.

Balharry, D. (1993): Social organization in martens: an inflexible system? Symp. Zool. Soc. Lond. **65**, 321–345.

Bontemps, J.; Houssier, C.; Fredicy, E. (1975): Physico-chemical study of the complexes of '33 258 Hoechst' with DNA and nucleohistone. Nucleic Acids Res. **2**. 971–985.

Brinkmann, B.; Rand, S.; Wiegand, P. (1991): Population and family data of RFLP's using selected single- and multi-locus systems. Int. J. Legal Med. **104**, 81–86.

Clevenger, A. P. (1993): Pine marten (*Martes martes* L.) home ranges and activity patterns on the island of Minorca, Spain. Z. Säugetierkunde **58**, 137–143.

Clutton-Brock, T. H. (1991): The Evolution of Parental Care. Princeton: Princeton Univ. Press.

–; Harvey, P. H. (1978): Mammals, resources and reproductive strategies. Nature **273**, 191–195.

Davies, N. B. (1991): Mating systems. In: Behavioural Ecology. Ed. by J. R. Krebs and N. B. Davies. London: Blackwell SP. Pp. 263–294.

Degener, P. (1918): Die Formen der Vergesellschaftung im Tierreich. Leipzig: Veit und Camp.

Gilbert, D. A.; Lehman, N.; O'Brien, S. J.; Wayne, R. K. (1990): Genetic fingerprinting refects population differentiation in the California Channel Island fox. Nature **344**, 764–767.

Gittleman, J. L.; Harvey, P. H. (1982): Carnivore home-range size, metabolic needs and ecology. Behav. Ecol. Sociobiol. **10**, 57–63.

Goethe, F. (1964): Das Verhalten der Musteliden. Hdb. Zool. VIII, 10. Teil, 1–80.

Heptner, V. G.; Naumov, N. P. (1974): Die Säugetiere der Sowjetunion. Bd II. Jena: G. Fischer. Pp. 538–571.

Jeffreys, A. J.; Wilson, V.; Thein, S. L. (1985): Hypervariable "minisatellite" regions in human DNA. Nature **314**, 67–73.

Kirby, L. T. (1990): DNA Fingerprinting – an introduction. New York: Stockton Press.

Kleiman, D. G. (1977): Monogamy in mammals. Quart. Rev. Biol. **52**, 39–69.

Krüger, H.-H. (1990): Home ranges and patterns of distribution of stone and pine martens. Trans. Inst. Union of Game Biol., Congr. **19**, 348–349.

Marchesi, P. (1989): Écologie et comportement de la martre (*Martes martes* L.) dans le Jura Suisse. Thèse doct. Université de Neuchatel.

McNab, B. K. (1953): Bioenergetics and the determination of home range size. Am. Nat. **97**, 133–140.

Monte, M. de; Roeder, J.-J. (1990 a): Histological structure of the abdominal gland and other body regions involved in olfactory communication in pine martens (*Martes martes*). Z. Säugetierkunde **55**, 425–427.

– (1990 b): Les modalités de communication chez la martre (*Martes martes*). Mammalia **54**, 13–24.

– (1993): Scent marking and social relationships in pine martens (*Martes martes*). Zoo Biol. **12**, 513–523.

Moors, P. J. (1980): Sexual dimorphism in the body size of mustelids (Mammalia: Carnivora): The role of food habits and breeding systems. Oikos **34**, 147–158.

Pulliainen, E. (1980): Winter habitat selection, home range and movements of the pine marten (*Martes martes*) in a Finnish Lapland forest. In: Worldwide Furebearer Conf. Proc. Ed. by J. A. Chapman and D. Pursley. Pp. 1068–1087.

– (1982): Scent-marking in the pine marten (*Martes martes*) in Finnish Forest Lapland in winter. Z. Säugetierkunde **47**, 91–99.

– (1984): Use of the home range by pine martens (*Martes martes* L.). Acta Zool. Fennica **171**, 271–274.

Sambrook, J.; Maniatis, T.; Fritsch, E. F. (1982): Molecular cloning. A new laboratory manual. Cold Spring Harbour, New York: CSH Laboratory Press.

Sandell, M. (1989): The mating tactics and sparing patterns of solitary carnivores. In: Carnivore Behavior, Ecology, and Evolution. Ed. by J. L. Gittelman. London: Chapman and Hall. Pp. 164–182.

Schacker, U.; Schneider, P. M.; Holtkamp, B.; Bohnke, E.; Fimmers, R.; Sonneborn, H. H.; Rittner, C. (1990): Isolation of the DNA minisatellite probe MZ 1.3 and its application to DNA 'Fingerprinting' analysis. Forensic. Sci. Int. **44**, 209–224.

Schmidt, F. (1934): Über die Fortpflanzungsbiologie vom sibirischen Zobel (*Martes zibellina* L.) und europäischen Baummarder (*Martes martes* L.). Z. Säugetierkunde **9**, 392–403.

– (1943): Naturgeschichte des Baum- und des Steinmarders. In: Monographien der Wildsäugetiere. Ed. by D. Müller-Using. Leipzig: Schöps.

Schröpfer, R.; Biedermann, W.; Szczesniak, H. (1989): Saisonale Aktionsraumveränderungen beim Baummarder *Martes martes* L. 1758. In: Populationsökologie marderartiger Säugetiere. Wiss. Beitr. Univ. Halle **37**, 433–442.

Storch, I. (1988): Home range utilization by pine martens. Z. Jagdwiss. **34**, 115–119.

Stubbe, M. (1969): Die analen Markierungsorgane der *Martes*-Arten. Acta Theriol. **22**, 303–312.

Wickler, W.; Seibt, U. (1983): Monogamy: an ambigous concept. In: Mate choice. Ed. by P. Bateson. Cambridge: Cambridge Univ. Press.

Wiegand, P.; Rand, S.; Bajanowski, T. (1992): Möglichkeiten der DNA-Typisierung an exhumierten Leichengeweben. Rechtsmedizin **3**, 13–15.

Authors' address: Prof. Dr. R. Schröpfer, Dr. P. Wiegand, and Dipl.-Biol. H.-H. Hogrefe, Department of Biology/Chemistry: Ethology, University of Osnabrück, Barbarastr. 11, D-49069 Osnabrück

Z. Säugetierkunde **62** (1997) 219–238

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Acoustic communication in the aardwolf, *Proteles cristatus* (Carnivora: Hyaenidae)

By G. Peters and A. Sliwa

Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany and Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa

Receipt of Ms. 01. 11. 1996
Acceptance of Ms. 13. 02. 1997

Abstract

Acoustic signalling behaviour of free-ranging and captive adult and juvenile aardwolves (*Proteles cristatus*) is described, based on sonagraphic analyses of vocalizations and behavioural observations. In addition to relying heavily on olfactory communication, the aardwolf uses diverse acoustic signals when interacting with conspecifics at close and medium range but seems to lack a true long-range vocalization. Vocalizations during agonistic interactions are the most diverse. About half of the species' 9 sound types presently documented belong to graded systems of sounds while the rest probably represents discrete types. It is not yet fully established whether all sound types listed actually function as acoustic communication signals. As far as data are available the acoustic signal repertoire of aardwolves is considerably different from those of the other species of the Hyaenidae.

Introduction

Various studies present data on acoustic communication in the four extant species of the Hyaenidae (taxonomy according to Wozencraft 1993). This is especially true for the spotted hyaena (*Crocuta crocuta*) (Kruuk 1972; Schaller 1972; Henschel 1986; Mills 1990; East and Hofer 1991 a, b). Considerably less is known of vocalization in the brown hyaena (*Parahyaena brunnea*) (Owens and Owens 1978; Mills 1982, 1990), the striped hyaena (*Hyaena hyaena*) (Kruuk 1976; Rieger 1981; Peters 1984), and especially the aardwolf (*Proteles cristatus*) (Koehler and Richardson 1990). While the spotted hyaena is probably one of the most vociferous terrestrial carnivores, the other hyaenid species are considered comparatively silent (Kruuk 1976) and the aardwolf particularly so (Kingdon 1977; Koehler and Richardson 1990; Estes 1991). Nevertheless, a number of different sounds uttered by this species are mentioned in the literature (e. g. Shortridge 1934; Smithers 1971; Estes 1991), all of them described in a non-quantitative manner and in terms inconsistent with terms used in this and other hyaenid species. The purpose of the present study is to give a first quantitative survey of acoustic communication in the aardwolf, including an outline of those aspects of its vocalization behaviour where data are lacking.

Material and methods

In the course of a 28 months field study on the game farm 'Benfontein', situated 10 km south-east of Kimberley, in the Northern Cape Province, South Africa, between May 1991 and August 1993 13 adult aardwolves (6 females, 7 males) were captured by remote immobilisation and fitted with radio-transmit-

ters. After an initial habituation period of two weeks, one of the authors (A. S.) followed them at night-time in a four-wheel-drive vehicle at a distance of 15–30 m, always in visual contact, aided by the vehicle's headlights and a low-powered hand held spotlight. Notes on the aardwolves' behaviour while vocalizing were recorded on a dictaphone. The volume of the different vocalizations was rated subjectively on an increasing scale from I to V, according to the distance over which they were audible for the human observer under calm conditions (I: 0–10 m; II: 10–20 m; III: 20–30 m; IV: 30–100 m; V: 100–200 m). Recording distances in the field varied between 15 and 40 m of the animal from the switched-off vehicle. Sound recordings were obtained with a Nagra IV-D tape recorder and microphone ECM 1035 AOI Super Cardonic Directional Microphone with windshield at a tape speed of 19.05 cm/second. The relatively great distance and the windy conditions limited the number of recordings which could be analysed and affected the scope and significance of measurements that could be obtained from spectrographic analysis. Vocalizations of three adult females and two adult males were recorded with a quality sufficient for sound spectrographic analysis. Several sounds of one hand-raised female aardwolf cub were recorded at distances between 10 cm and about 2.5 m with an AKG D202 ES microphone without windshield and the same tape recorder and recording speed as described above when it was 5 and $8^1/_2$ months old. Both microphones used have a reasonably flat frequency response in the range of the vocalizations studied. Sound spectrographic analyses were done on a MEDAV SPEKTRO 3 000, version 3.2, 1991. Sonagraph settings for frequency and time ranges and resolutions were chosen according to the structural parameters measured for each vocalization type and can be gathered from the sonagrams figured. Oscillograms of all vocalizations analyzed were checked to avoid overloading. Pulse repetition rate was calculated according to method B given by Scoville and Gottlieb (1978). The calculation was based on number of pulse pairs per train in sounds with pulse pairing and on single pulses in those without pairing. Heavy background noise was removed by filtering if, according to the sonagram, the vocalization appeared to have no frequency components within the range filtered. Filtered sonagrams are identified as such in the figures and details of filtering are given. General structural parameters of the different vocalization types are presented in Table 2. As our sample is relatively small these are unlikely to reflect the whole range of structural variability of the species' vocalizations and/or may not be fully representative for certain vocalization types.

Results

Throughout this publication the term "vocalization" is used for any (communicatory) sound produced by aardwolves, irrespective of whether it is voiced or unvoiced and regardless of mode of sound production. The vocalizations of the aardwolf will be described in a uniform format for juveniles and adults. We first present the types established on the basis of spectrographic analysis. We then describe those for which few or no recordings are available but the observer witnessed them frequently and their occurrence in specific behavioural contexts was typical and fairly common.

We identified nine different vocalizations: "purr", whine, jaw click, lip smack, snarl, growl, bark, squeal, and a whizzing sound (see Tabs. 1, 2). Only for the last vocalization type the description and classification is solely based on the observer's (A. S.) auditory impression.

"Purring"

At about 4 weeks of age a hand-raised female aardwolf cub was heard to produce a fairly sustained, low-pitched, vibrating sound when stroked or when in body contact with her foster parents, in many respects reminiscent of the purring of a domestic cat. Addressees under natural conditions are very probably siblings and/or parents at very close distance. "Purring" probably signals comfort – if it serves a communicatory function at all. A more regular, sustained and more intense production of this sound seemed to reflect the animal's continuing comfort.

The sound was observed repeatedly during the animal's juvenile development and was still present when she was given away at 9 months of age. Then the sound could be heard

up to several meters away, being considerably louder than felid purring. Aardwolf "purring" (Fig. 1 a–c) is rather constant in pitch and can go on for minutes, sometimes with very short interruptions of sound production at irregular intervals. Sound intensity varied but there was no regular pattern in this respect, nor was there a regular alternation of sound quality as in felid purring where sound quality differs between exhaling and inhaling. Thus we could not ascertain whether sound production occurred during exhalation and/or inhalation, but exhalation is considerably likelier. During vocalizing the vibration of the body surface was palpable, especially on the chest, neck and abdomen. This vocalization was not observed in the field, neither in juveniles nor in adults, probably because of the large observation distance or because it is only produced while the animals are in the den. "Purring" occurred only at intensity level I. The term "purring" for this aardwolf vocalization is deliberately used in inverted commas to signify that based on the available analysis data it seems to differ from felid purring as will be detailed below.

Three continuous recordings of aardwolf "purring" were available for analysis, recorded once when the captive juvenile female was 5 months old. Thus no comments can be made whether its structure undergoes ontogenetic change. These examples of "purring" lasted 30.59 s, 33.07 s and 40.59 s with fairly sustained vocalization, traceable sound production being present for 66.8%, 70.9% and 57.4% of the total recording. Aardwolf "purring" is composed of largely continuous pulse trains of varying duration with a more or less regular sequence of the single pulses (Fig. 1 a). In our recorded sample intervals without sound production between pulse trains lasted between 0.13 and 2.66 ($\bar{x} = 0.6 \pm 0.39$) s (n = 62). The recorded pulse trains consisted of 2–36 ($\bar{x} = 15.14 \pm 10.9$) (n = 65) single pulses. No regular pattern in the occurrence of these pulse trains was discernible. Of the 65 pulse trains analysed in the whole "purring" sample 28 (43.1%) consisted of ≤ 8 (x = 4.36 ± 1.22) pulses and had an average duration of $\bar{x} = 0.2 \pm 0.11$ s; the remaining 37 (56.9%) pulse trains consisted of ≥ 12 ($\bar{x} = 18.7 \pm 11.1$) pulses and had an average duration of $\bar{x} = 1.65 \pm 0.78$ s.

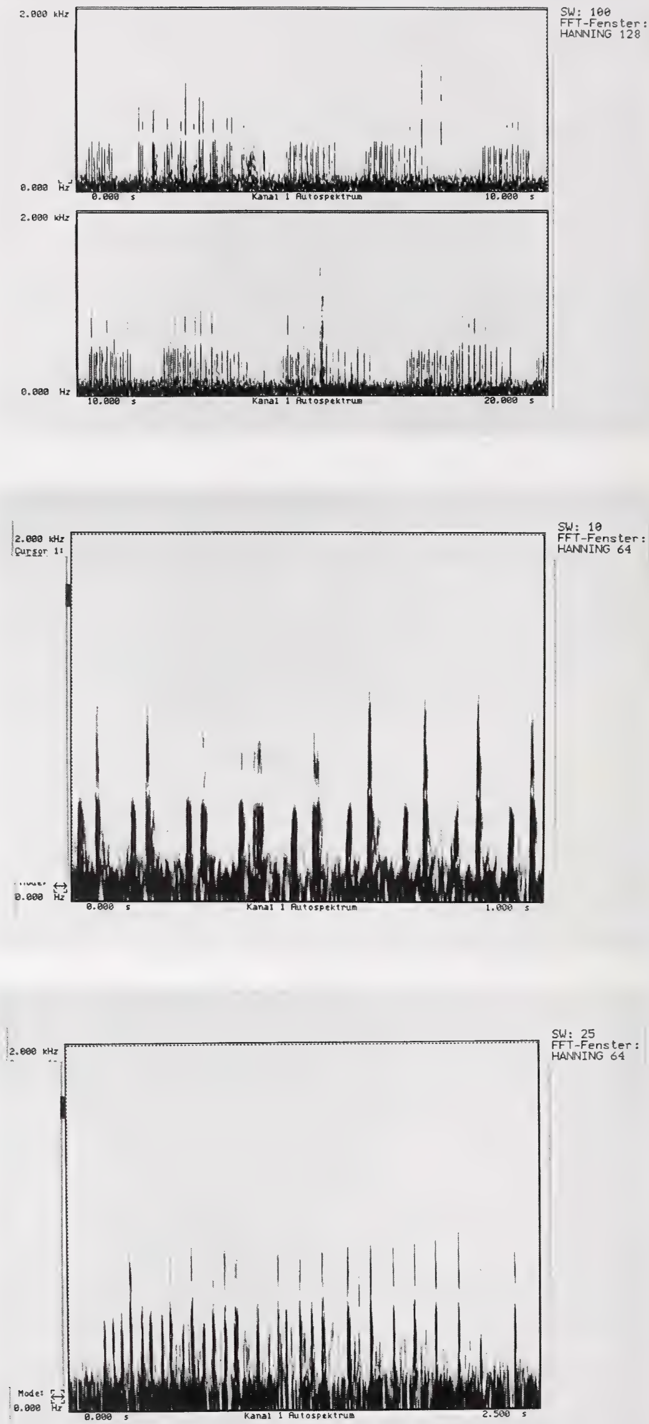
If each phase without sound production and the subsequent vocalization phase are considered as one "breath", representing one coherent inspiratory (without sound production) and expiratory phase (with sound production), average "breath" duration of this juvenile aardwolf while producing "purring" would be 1.72 s, resulting in an average rate of 34.9 "breaths" per min during the production of this sound. It seems unlikely, though, that each of the very short pulse trains in our recordings of "purring" represents a complete exhalatory phase, and the short phases without sound production directly preceding and following such a pulse train inhalatory phases accordingly.

The sequence of pulses is not regular throughout the duration of a train. Single pulses may be of variable intensity. For varying portions of the duration of the pulse trains, pulses are paired off (Fig. 1 b). During other portions of the pulse trains pulse pairing is less obvious, or they are sequences of single pulses with pulse repetition rates equivalent to the repetition rates of the pulse pairs (Fig. 1 c). Pulses and pulse pairs occurred at a rate of 7.1 – 9.9 ($\bar{x} = 8.47 \pm 0.62$) (n = 28) per s. Because of heavy background noise and high input level during the original recording it is not clear whether the energy maximum

---

▶

Fig. 1. Aardwolf "purring" by a juvenile ♀ 5 months old.
a: A continuous 20 s stretch (upper plus lower sonagram) of "purring" with more or less regularly structured pulse trains of varying duration interrupted by phases without sound production which may represent phases of inhalation.
b: A stretch of 1 s of "purring" with clear occurrence of pulse pairs, nine of which are present here.
c: Another stretch of 2.5 s duration with a less regular sequence of pulses with pulse pairs in the beginning portion and single pulses in the end. These follow each other at about the same repetition rate as the preceding pulse pairs.


2.000 kHz
SW: 100
FFT-Fenster:
HANNING 128
0.000 Hz
0.000 s
Kanal 1 Autospektrum
10.000 s
2.000 kHz
0.000 Hz
10.000 s
Kanal 1 Autospektrum
20.000 s
2.000 kHz
SW: 10
FFT-Fenster:
HANNING 64
0.000 Hz
0.000 s
Kanal 1 Autospektrum
1.000 s
2.000 kHz
SW: 25
FFT-Fenster:
HANNING 64
Mode:
0.000 Hz
0.000 s
Kanal 1 Autospektrum
2.500 s

a

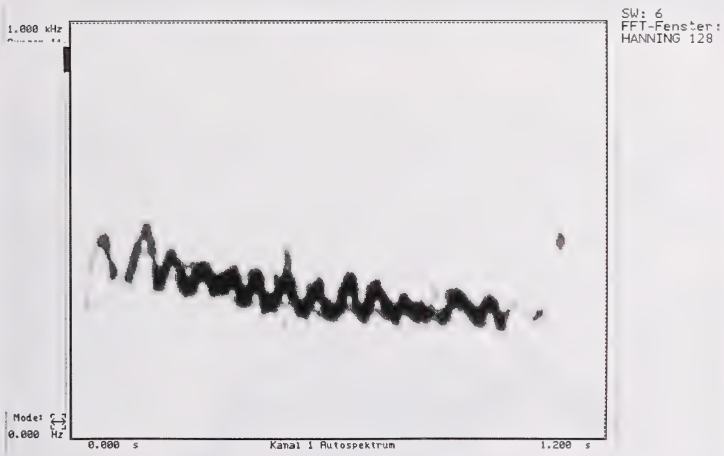
b

c

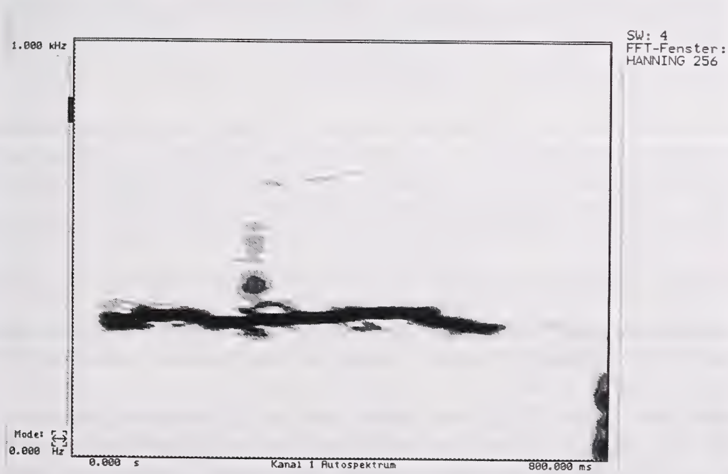
of “purring” at about 40 Hz actually belongs to this sound. The cause of the differences in pulse structure is unknown. On the basis of the available data it is not possible to make a statement as to the detailed mechanism of sound production in aardwolf “purring” as compared to that of felid purring (Frazer Sissom et al. 1991). Very likely “purring” is a discrete type of vocalization.

Whine

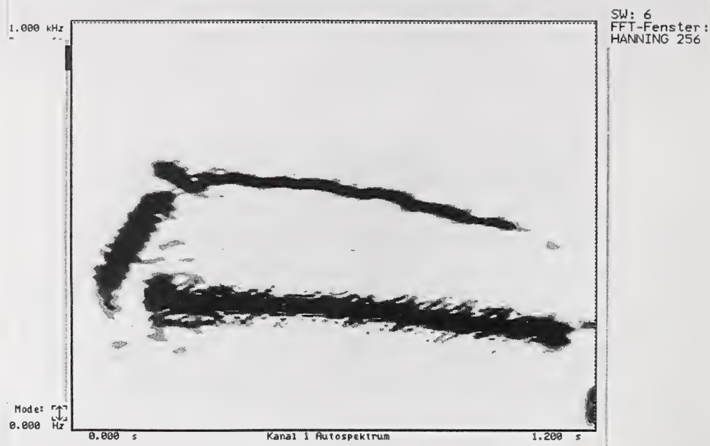
Whines (Figs. 2 a–d) are clear tonal calls of variable pitch and degree of frequency modulation (FM). Most whines decrease slightly in pitch towards their end, usually after a short and variable increase in pitch in their beginning. They are comparatively short sounds. Relatively loud whines could be clearly heard for over 100 m but much softer whines also occurred. On one occasion a male followed the scent-marks of a receptive female and when sensing her proximity whined loudly while trotting about 100 m past



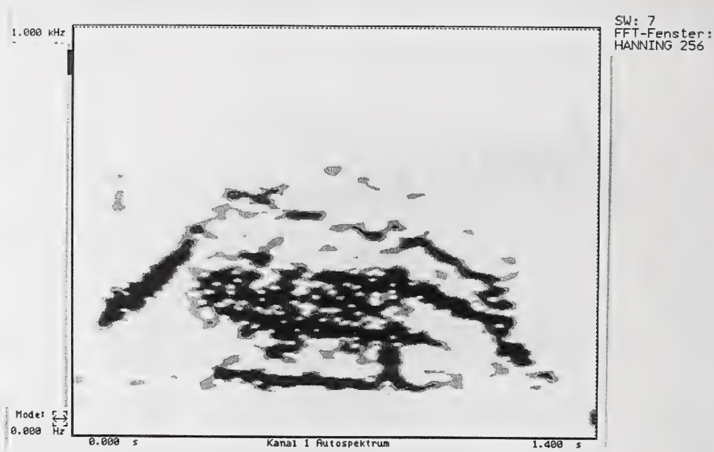
a



b



c



d

Fig. 2. Whines of adult ♂ aardwolves. Because of adverse recording conditions unequivocal designation of frequency bands (as f0, f1, f2, etc.) showing in the spectrograms is not always possible.
a: Higher-pitched variant of this call with distinct and fairly constant periodical frequency modulation (FM) for the whole of its duration (high-pass filtered >250 Hz).
b: Another variant of higher-pitched whine with little FM which is not periodical (high-pass filtered >280 Hz).
c: Low whine with two harmonically related frequency bands and an incipient sound (band-pass filtered for range 170–700 Hz).
d: Low whine with (at least) 4 harmonically related frequency bands (and likely subharmonics) for a portion of its duration and an incipient sound (band-pass filtered for range 110–690 Hz).

where she was lying behind a hill out of sight from him. Upon hearing him she jumped up and ran after him, caught up and immediately mated with him. Less loud whines were heard from males approaching the den containing the female and cubs when they took up guarding duties. Then they were usually uttered at about 50 m from the den and always

when catching sight of the female lying outside of her den. Males also used a soft and high-pitched whine audible for about 30 m repeated up to six times within an interval of about 2 min when trying to solicit eight weeks and older cubs to follow them on short excursions around the den, or when they moved too far from the den when they were older. Males also whined softly when cubs approached to greet them. Females whined when approaching the den after a foraging trip and to solicit cubs to follow them on short foraging trips. When the cubs were still in the den, females used whines to call them out (P. R. K. Richardson, M. D. Anderson pers. comm.). Whines were never heard between two adult males or from cubs towards their parents. Whining outside the mating season was produced mainly by males towards juveniles. Females whined less often and were never heard to produce loud whines towards adult males over longer distances. The intensity of whines rated as level II–IV (for the most intense forms). Whining was used during friendly contact at close and approach at close to medium range. It probably functions as an appeasing and reassuring sound. The reaction of the addressee is in cubs to come out of the den and/or follow when their mother or father whines. A female's reaction to male whining during the mating season was related to her reproductive status. She either rebuffed him vocally and/or actively or followed him. All whines recorded and analyzed were those of ♂♂ during the mating season.

The human observer can roughly classify these calls into two categories according to their pitch: a lower-pitched and a higher-pitched form. The latter can be differentiated further on the basis of FM. This classification does not encompass all whines recorded on tape; some calls were intermediate in pitch or FM. Sonagraphic analysis largely supports this preliminary distinction. We analyzed 11 calls for one variant of higher-pitched and 10 in the other, and 12 calls of the lower-pitched form. Additionally, 4 intermediate calls were provisionally classed with the category they were closest to structurally, 3 with the higher-pitched and 1 with the lower-pitched variant.

Periodical FM was obvious in one variant of the relatively higher-pitched whines (Fig. 2 a) in which only one frequency band is present; it is likely to be the fundamental. FM over the whole duration of the call varied but in the majority of these whines the frequency decreased towards the end of the call. Periodical FM occurred at a rate of 15–20 Hz but was not fully regular in its temporal and frequency characteristics for the whole duration of the call. The frequency change during one FM period of about 60 ms duration can be more than 200 Hz. The other variant of relatively higher-pitched whines usually also showed one frequency band only (probably the fundamental) with variable overall FM but no periodical FM (Fig. 2 b). In the three calls provisonally grouped with this whine variant more than one frequency band showed up in the sonagram.

Lower-pitched whines (Figs. 2 c, d) usually show 2–4 frequency bands, 2 harmonics (with a ratio of their frequency components of 1 : 2) usually being significantly more intense than the other (Fig. 2 d). Of the 12 examples analyzed of this form of whine 8 had an initial sound (Figs. 2 c, d) of approximately 0.2 s duration (an average of a little less than 20% of the whole duration of the call). The initial sound consisted of only one steeply ascending frequency band (no additional harmonic as in the rest of the call) with a frequency difference of about 200 Hz between its start and end. In addition to the structural diversity of the calls classified as whines in this study (all recorded in the same general behavioural context), the diverse other functional contexts in which whines occur strongly suggest that further differentiation of this category is appropriate. However, a complete and fully substantiated subdivision of whines or even a division of this category into several vocalization types requires more structural and behavioural data than are available at present. We are still unsure whether they belong to a graded call system or represent discrete vocalizations but the former is more likely.

Jaw click

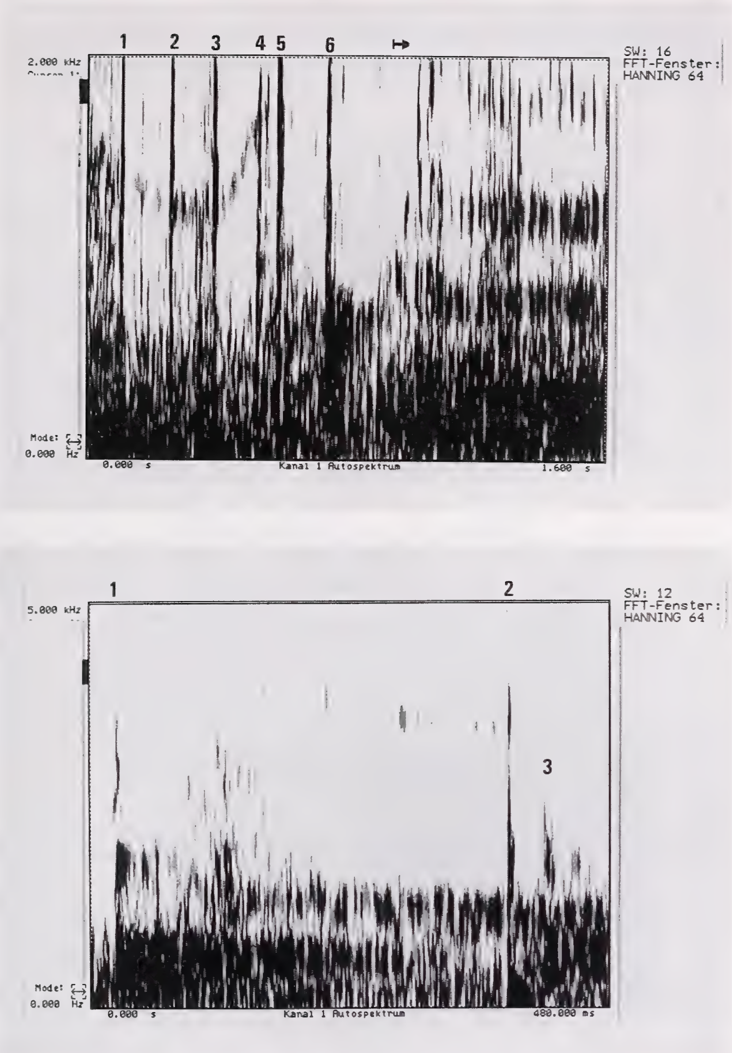
Muffled sounding clicks were heard at close quarters when an animal was growling. They were audible over about 10 m and thus rated I–(II) on the subjective volume scale. They were most likely generated through forceful closing of the jaws, the clash of the teeth producing the sound. Jaw clicks were used in intra- and interspecific threat behaviour, interspersed with growling or snarling and occurred in conjunction with lip smacks (see below) as opening and closing sounds of the jaws and lips. Usually several of these sounds were produced in a row. Jaw clicks were only witnessed in a wild adult male approached on foot by the observer at about 10 m and in the $8^1/_2$ months old captive female cub when another similar aged male cub approached her. It is not clear whether jaw clicks function as a real acoustic signal or whether they are just a by-product of the closing of the jaws indicating an intention to bite. In a series of 5 jaw clicks (Fig. 3 a) the first 4 clicks follow each other at intervals of about 130 ms, the last click which is weaker than the preceding clicks occurred after an interval of about 50 ms. Jaw clicks represent a discrete sound type.

Lip smack

Lip smacking occurs in the same circumstances and often occurs together with jaw clicks (Fig. 3 a), interspersed between growling or snarling stretches, during intra- and interspecific threat behaviour. We have one recording of a lip smacking sequence without jaw clicks being present in it (Fig. 3 b). Lip smacks, jaw clicks and slight growling where heard once when the observer (A. S.) approached a habituated adult male aardwolf on foot. The animal looked at the observer and opened and closed its lips with a smack, audible for at least 10 m. The other incidence of lip smacking was when a hand-raised female cub was approached by a male cub. The volume of the sound is equivalent to I(–II) on the subjective volume scale. A smacking sound is generated through forceful closing and/or opening of the jaws, lips and cheeks probably contributing to sound production. As with jaw clicks it was not clear whether it functions as an acoustic signal or was an acoustic by-product of the opening and closing of the mouth. At present it is not possible to separate jaw clicks and lip smacks unequivocally on the basis of sound structure. There is a minor clue in the sound quality, that of jaw clicks is relatively harder and more mechanical than lip smacks. The two examples analyzed were recorded in the juvenile ♀ aardwolf when it was $8^1/_2$ months old. In the one sound sequence where both vocalization types seem to occur together we interpret the last sound after a preceding series of 5 jaw clicks as a lip smack (Fig. 3 a). It follows the last jaw click after an interval of about 140 ms. The other series (Fig. 3 b) consists of three sounds without accompanying jaw clicks. The interval between the first two is about 350 ms, that between the second and third sound only about 24 ms. The frequency components with maximum amplitude in lip smacking cannot be established with certainty because the lower frequency range <1 kHz is affected by heavy background noise. Like jaw clicks, lip smacks represent a discrete vocalization type with probably little structural variability. Despite their close temporal association and occurrence in the same behavioural contexts, and the problems in separating them they are listed as distinct sound types because they are produced by different body structures.

Growl

Aardwolf growling is similar to the growl of other terrestrial carnivores. It is a fairly continuous low rumbling, throaty "rrrrrrrrrrr" sound, variably sonorous and usually sustained for some time. It is quite similar to the growling of a large sized dog and is usually louder and sounds more "impressive" than would be expected for a mammal of an aardwolf's size. Its high intensity forms were audible at a distance of up to about 20–30 m, its

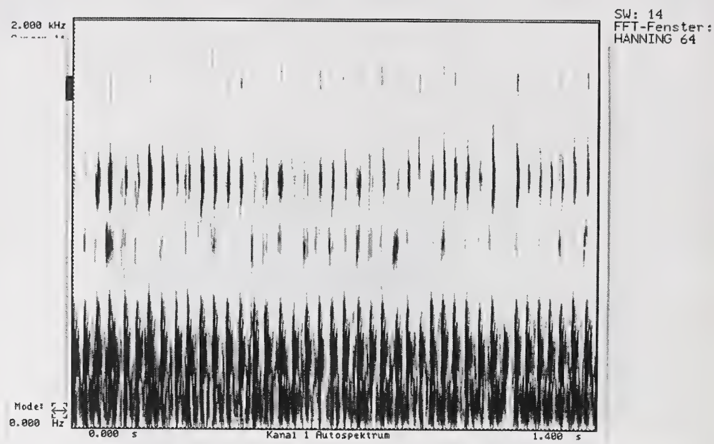


a

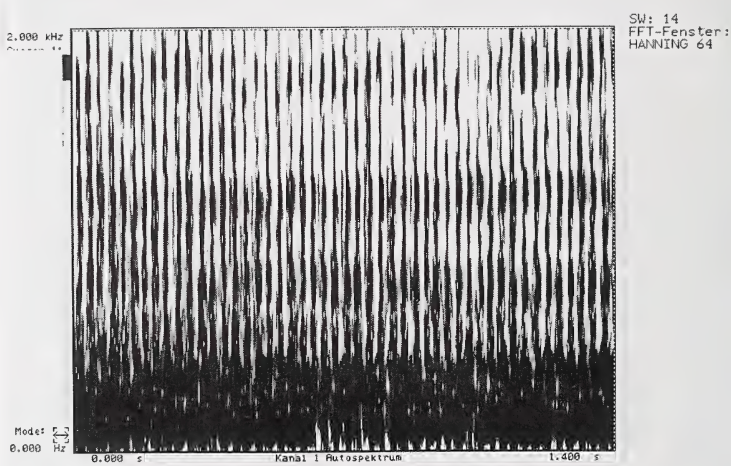
b

Fig. 3. a: Five jaw clicks (marked '1' to '5') and one lip smack (?) ('6') of a juvenile ♀ aardwolf $8^{1}/_{2}$ months old. They are directly followed by growling the start of which is marked by an arrow. b: A sequence of 3 lip smacks (marked '1' to '3') of the same individual. In both sound sequences the positive identification and distinction of the two vocalization types is still equivocal, though. Both recordings with heavy background noise.

intensity is rated at II–III on the subjective scale; low intensity forms of growling rate at level I. Growling at low to medium intensity and relatively short duration was produced during expiration only, the longer phases of expiratory sound production interrupted by only relatively short phases of inspiration without vocalization. Sometimes a sound was also produced during inspiratory phases. With increasing duration and intensity sound production was more likely to continue over the short inspiratory phase between two adjacent expiratory phases. These voiced inspiratory phases in growling sounded like inspiratory snarling and are very similar to it in structure, indicating a close relationship



a



b

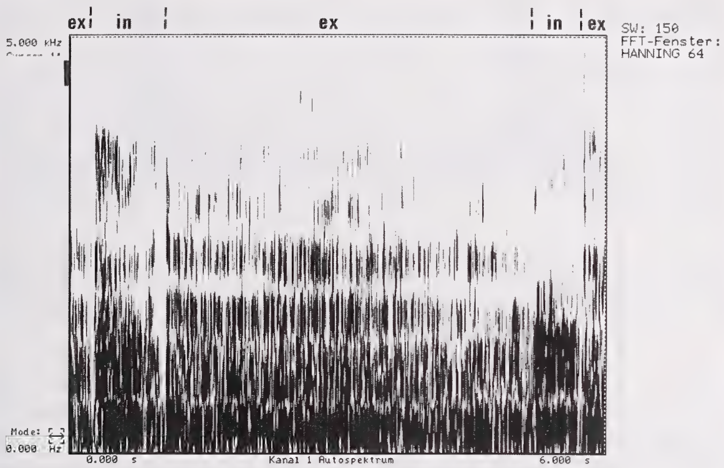
Fig. 4. Growling of a juvenile ♀ aardwolf $8^1/_2$ months old.
a: Growling of little sonority with clear representation of single pulses.
b: Growling of higher sonority in which the single pulses are not as distinct as in a. and less well separated from each other.

between growling and snarling. Nevertheless, we prefer to separate growling proper here from snarling proper. The criteria to separate the 'pure' forms of the two vocalization types are listed in the section on snarling.

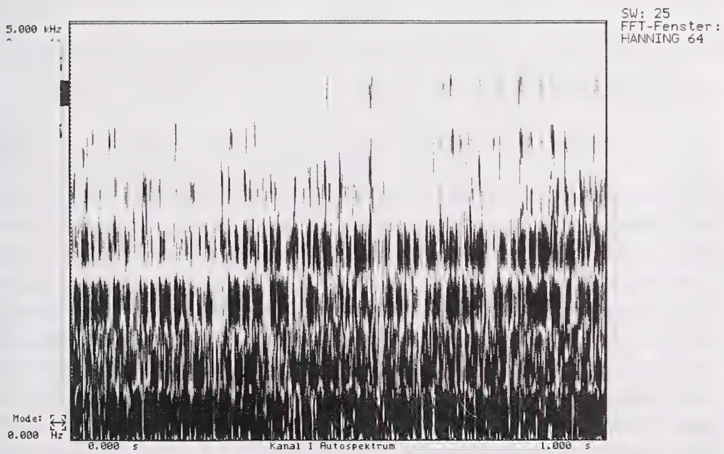
Growls were used as a defensive threat towards conspecifics and heterospecifics, usually together with snarls, and often preceding barks. Aardwolves seem to lack an acoustic signal of offensive threat; attacking individuals were always silent with the exception of the whizzing sound in one individual (see below). In the wild growling was most often heard during the mating season when females growled at courting males who tested their receptivity through slight and short attacks (RICHARDSON 1985, 1987). It was used

throughout the year and heard first in wild cubs at 6 weeks of age. As in the three other vocalizations that occur during agonistic behaviour (snarling, jaw click, lip smack) growling could only be analysed in a juvenile ♀ $8^1/_2$ months old. Our subjective acoustic impression is that the structure of these vocalization types in animals of this age is very similar to that in adults.

Growling (Figs. 4 a, b) of variable intensity and sound character can go on for 10 s and more without interruption of sound production. Short (inspiratory) intervals of at least 1 s duration interrupted sound production but several inspiratory and expiratory phases of sound production could also follow each other without interruption of vocalization. The



a



b

Fig. 5. Snarling of a juvenile ♀ aardwolf $8^1/_1$ months old.

a: A stretch of 6 s with continuous sound production during in- and expirative phases of respiration (marked 'in' resp. 'ex').

b: One second of expirative snarling. Pulsation is less pronounced, single pulses are much less clearly separated and the structure of the sound is noisier than in growling.

sonority of the sound changed over its duration. Pulsation was very obvious and regular in the exhalatory phases of growling with a pulse repetition rate of 30–35 pulses per s. The inhalatory phases were much less clearly pulsed; a pulse repetition rate could not be determined.

Snarl

Snarls are louder, distinctly more voiced and rather more tonal, higher in pitch, and much less clearly and regularly pulsed than growls (Fig. 5 b); short, intense outbursts may sound like a roar. Aardwolf snarls are very similar to snarls of a large dog, rating at III on the subjective volume scale in its most intense forms. Like growling snarling is a sustained vocalization usually continued for some time. However, contrary to growling, sound production generally occurred during both in- and expiratory phase of respiration, although it was not necessarily continuous during both phases (Fig. 5 a). Inspiratory phases of snarling were higher in pitch and much shorter than the expiratory phases. Together with growling and barks, snarls of aardwolves were heard during intra- and interspecific agonistic encounters and were part of the species' defensive display. The sender seemed to be more strongly agitated than during growling, resulting in more hectic vocalizing. Snarling was usually uttered in agonistic situations at close range as a high-intensity defensive threat, rising out of a growl and, with withdrawal of the addressee, tapering off into a growl again. If the opponent further approached snarling broke and rose into a bark or a short series of barks. Snarling was only heard during serious agonistic encounters when the opponent of the sender attempted to bite or make physical contact. It was first heard when juveniles were about eight months old but it is very likely that it is already present much earlier during ontogeny. In adults it was heard from both sexes during fights and in the mating season when the sender was pressed hard, as females having to defend themselves against frustrated courting males (Sliwa 1996) or males fighting over mating rights of females (Richardson 1987).

Stretches of fairly continuous snarling lasted for up to 20 s. A concentration of sound energy in broad, somewhat noisy frequency bands was visible in the sonagrams, an indication of the more voiced and tonal character of snarling compared to growling and the differences between the two respiratory phases. We currently assume that snarling and growling form a graded sound system.

Bark

Barks in aardwolves were the loudest form of defensive vocalization. The barks were often heard over 200 m distance, and could even be heard when the animal was deep down in a den. We rated them at IV–V on our subjective intensity scale. Barks varied in sound from a hoarse cough to a fully explosive bark. They were relatively deep like that of a large-sized dog. Barks were most often heard in the wild during the mating season. Females barked at males testing their receptivity through little attacks. Barks of the female coincided with lunges of the testing male. They usually grew out of a preceding growl or snarl and generally tapered off into growling and/or snarling. The addressee was more likely to retreat when the sender barked, and if the addressee did not retreat, actual fighting proceeded. Increasing stress, like the approach of the addressee, led to a higher repetition rate of barks. Barks were first heard in six weeks old cubs. During territorial encounters only the chased animal barked defensively. During a serious fight of two adult males at the height of the mating season, only some low intensity growling was heard. Females whose receptivity was tested by males through circling around them and slight attacks growled continuously and often barked on seeing the male approach from 10 m away. Most of the recorded barks were produced by females in their dens. Very few barks

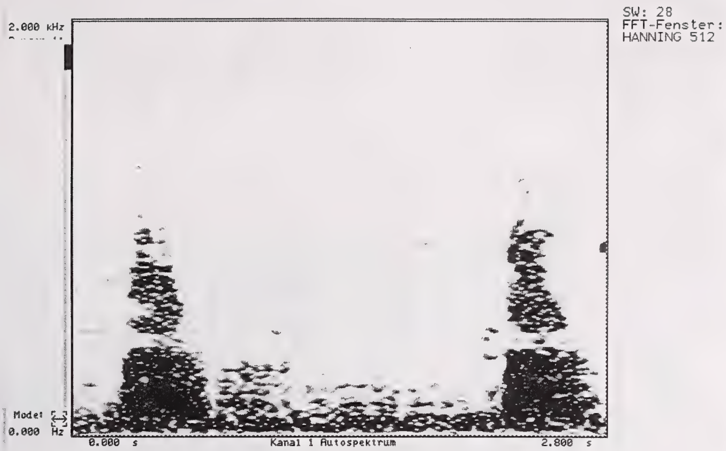


Fig. 6. Two barks of an adult ♀ aardwolf. Structural characteristics of this vocalization type as showing in the sonagram are affected by the fact that the animal was recorded while vocalizing in its den. The original duration of the interval of about 15 s between these barks was shortened in the analysis. Recording with high level of background noise.

could be recorded in animals which were above ground but all of these were so far away from the observer that the recording quality was poor. Therefore the material on which the structural analyses are based is limited. Barks (Fig. 6) were short sounds. Their frequency distribution was atonal.

Squeal

Handling the feeding bowl at feeding time caused the hungry hand-raised aardwolf cub to give a loud, sometimes staccato-like squealing sound, in anticipation. These squeals increased to a more continuous loud squeal of a bleating quality with opened mouth which further graded into even louder continuous squeals with increasing frustration. Similar sounds could be heard when a mother returned to her den and the cubs were struggling to suckle. The volume varied between II and III on the subjective volume scale, the sender's mouth opening slightly with increasing intensity of squeals. They were heard in wild cubs of about three months at close quarters and in the hand-raised female cub at about two months and were still uttered when she was 9 months of age but they were never observed in adults. Squeals seem to have a begging role.

All recordings of squeals are of the ♀ juvenile at an age of 5 months. Their quality is poor due to background noise and therefore no sonagram is figured. Squealing can be interrupted into short staccato-like sounds but usually goes on for several seconds. Long stretches of squealing sounds can follow each other, only interrupted by short phases of inspiration. It is largely tonal and variable in pitch with up to 4 harmonics with some variable FM. In all calls the fundamental f0 is the most intense harmonic. Due to our limited sample and the poor quality of the recordings no statement can be made about the variability of these calls. It is also not clear whether squealing of juvenile aardwolves is a discrete or a graded sound type, although the latter is more likely. Possible structural relationships between squealing and whining cannot be clarified on the basis of our material.

Table 1. Vocal repertoire of aardwolves (*Proteles cristatus*). General characterization of vocalization types.

Vocalization type	Description	Frequency of occurrence	Sender	Behavioural contexts	Body posture and facial expression of sender	Reaction of addressee
"purring"	similar to domestic cat purr but not continuous	?	juvenile ♂♂ and ♀♀, adults ?	relaxed close contact	lying down, relaxed, eyes (halfway) closed	?
whine	short clear tonal sound of variable pitch	seasonally common	adult ♂♂ and ♀♀	sender approaching addressee	head low, body crouched or upright, varies with sound intensity, ears flattened	variable: no reaction → approach
jaw click	soft clicking sound	uncommon	♂♂ and ♀♀, subadults and adults (?)	addressee approaching sender	head low, ears flattened, hair erected	?
lip smack	soft smacking sound	uncommon	♂♂ and ♀♀, subadults and adults (?)	addressee approaching sender	standing errect, ears pointing forward	?
growl	fairly sustained low rumbling sound	seasonally common	♂♂ and ♀♀, all age classes	addressee approaching sender	head low, ears flattened, hair erected	variable: retreat → attack
snarl	similar to snarl of a dog or cat	seasonally common	♂♂ and ♀♀, all age classes	addressee approaching sender	head low, ears flattened, hair erected	variable: retreat → attack
bark	similar to bark of a large-sized dog	seasonally common	♂♂ and ♀♀, all age classes	addressee approaching sender	crouched, hair erected, mouth open	variable: **retreat** → attack
squeal	sustained high-pitched cry of variable intensity and tonality	?	juvenile ♂♂ and ♀♀	nursing	variable, moving, head stretched forward	caregiving, nursing
whizzing sound	hollow whistle sound	seasonal, uncommon (?)	adult ♀♀ (?)	sender approaching addressee	running, ears flattened	variable: no reaction → flight

Table 2. Vocal repertoire of aardwolves (*Proteles cristatus*). Structural characterization of vocalization types.

Vocalization type	Duration [s]	Frequency range [kHz]	Frequency distribution	Relatively intensive range [kHz]	Maximum intensity [kHz]	Generated during expiration inspiration	Main variable structural parameters	Comments
"purring" $n = 65$	0.07–3.67 $\bar{x} = 1.12 \pm 0.93$ (continuous pulse trains)	<1.8	atonal, pulsed	<0.14	0.04 ?	ex (+ in ?)	duration, pulsation	analyses adversely affected by low intensity
whine $n = 37$	0.44–1.86 $\bar{x} = 0.943 \pm 0.304$	<0.7	tonal	0.26–0.43	0.35	ex	pitch, frequency modulation	sample heterogeneous
jaw click	series: 0.5 (5 clicks) single click: 0.012	0–>5	atonal	<0.6 and 1–2.3	1.7	–	number of and intervals between single sounds in series	sample very small
lip smack	series: 0.4 (3 smacks) single smack: 0.013	0–>5	atonal	<0.85 and 1.5–2	?	–	number of and intervals between single sounds in series	sample very small
growl	–>10	<3	atonal, pulsed	<0.5	approx. 0.35	ex + (in)	duration, pulsation, sonority	
snarl	ex: 1.7–5.2 in: <1	–>4.5	atonal/(tonal), (pulsed)	<2	ex: 0.3 in: 0.38	ex + in	duration, tonality	
bark	<0.5	?–>4.5	atonal	0.1–1	approx. 0.5	ex	?	analyses insufficient
squeal	variable	0.2–1 ?	tonal/(atonal)	<0.5	0.24–0.42	ex	pitch, frequency modulation	sample very small
whizzing sound	approx. 2–3	?	tonal?	?	?	ex?	?	not tape recorded

Whizzing sound

A whizzing sound was heard during agonistic encounters of a female aardwolf running up to a 'courting' male, standing close, while facing away from the female. The sound is high-pitched, continuous for several seconds, ascending in pitch and fairly constant in its intensity. The female uttered this sound when starting to run fast and straight for the male, sound production stopping when reaching the male. It is somewhat reminiscent of a hollow whistle but we cannot liken it to a sound known to us in any other animal species. The whizzing sound is audible for at least 30 m thus ranking at III on the volume scale. When the male did not move away the female tried to bite him and sometimes a short low-intensity fight could ensue. In the context observed whizzing might function as an aggressive threat to warn the addressee of the immediate danger of physical attack. It is unclear how it is produced and whether it represents an acoustic signal. We were not able to record this sound in the wild and therefore are not able to describe it in a technical manner but it was heard more than 20 times in predictable circumstances. Nevertheless, as this whizzing sound was heard in only one female, although repeatedly during the mating season over three years, it cannot be ruled out that it represents an idiosyncrasy of this individual. Our observations do not allow a definite statement about its variability but the whizzing sound seems to be a discrete sound type.

Discussion

Being considered a solitary and relatively silent species (Kingdon 1977; Koehler and Richardson 1990; Estes 1991), only staying together with conspecifics for a brief period during the mating season and for considerable time while raising its cubs, the aardwolf's acoustic signal repertoire as described here appears to be fairly diverse, especially during agonistic behaviour. Although our data are limited they represent a considerable improvement of the previous state of knowledge and understanding of acoustic communication in this species.

Smithers (1971, 1983), Richardson (1985), Skinner and Smithers (1990), and Estes (1991) reported that when defending themselves and fighting aardwolves emit growls, hoarse barks, and roars of surprising depth and volume for such a small animal. It is likely that these vocalizations are equivalent to the agonistic sound repertoire described here as growling, snarling and barking. Koehler and Richardson (1990) mentioned a soft clicking sound produced by opening and closing of the mouth as the lowest form of threat. This fits well with the jaw clicks and/or lip smacks described in this study but these authors did not differentiate between two sound types. Cubs are said to make a clicking noise very much like the warning clicks of termites (Bartlett and Bartlett 1967), in addition to barking and growling softly (Smithers 1971). The latter two vocalizations were also observed by us but it is not clear what these clicks of cubs actually represent and whether they are connected with the jaw clicks mentioned by Koehler and Richardson (1990) and in the present study. For some aardwolf vocalizations mentioned in the literature it is difficult to correlate them with the species' acoustic signals as described in the present publication. Langden (in Shortridge 1934) reported on whistling calls between mates which may refer to the whines described here. According to Wilhelm (in Shortridge 1934) aardwolves have a howl similar to that of a striped hyaena. As no technical study of striped hyaena vocalization exists this statement cannot be assessed. Estes (1991) expressly stated that the three vocalization types warning clicks, whistle, and howl need confirmation but he did not specify on the basis of which evidence they are less likely to be actually present than the other ones mentioned in the literature. The vocalization types snarl and lip smack have not been expressly named

and described in the literature on the aardwolf before. It is likely that they were subsumed under growling and jaw clicking respectively. The following vocalizations cannot be identified from descriptions in the literature and hence constitute newly described types: "purr", squeal, whizzing sound. As no technical data are given for the vocalization type 'soft squeal' listed in juveniles and adults of the spotted hyaena by Kruuk (1972) and Mills (1990) it is not possible at the moment to establish its exact nature as compared to the juvenile aardwolf squeal described here. The same is true for various vocalizations termed 'snarl', 'growl' and 'whine' or variants of these in the striped (Kruuk 1976), spotted (Kruuk 1972; Mills 1990) or brown hyaena (Mills 1990). As vocalization types of different species in the same genus, family, and order ought to be given the same name only if they are homologous, the use of these terms in different species of the family Hyaenidae is preliminary.

It is well documented that intraspecific communication in aardwolves primarily relies on olfaction and scent-marking (Kruuk and Sands 1972; Richardson and Bearder 1984; Richardson 1990, 1991; Sliwa 1996). However, for immediate, short to medium range communication they possess a fair-sized repertoire of expressive visual and vocal signals. The size of the acoustic repertoire with its discrete sound types and graded vocalizations seems to be similar to those of *Hyaena* (Kruuk 1976) and *Parahyaena* (Mills 1990) but smaller than that of *Crocuta* (Kruuk 1972; Mills 1990). As all published information on vocalization in the three other species of the Hyaenidae is non-technical a comparison of their acoustic signal repertoires with that of the aardwolf can only be provisional. It cannot be ruled out that *Proteles* has more vocalization types than described here. This is especially true as close-range observations of females with cubs are lacking, and vocal communication generally plays an important role in this behavioural context in Carnivora, especially from the time when the young start to leave the den until they become independent (Peters and Wozencraft 1989). Moreover, a numerical comparison of acoustic repertoire size (as established by the human investigator on the basis of sonagraphic analysis) is unlikely to be a direct measure of the communicative potential the repertoire offers to the sender, especially if applied in combination with other signalling modes. In most behavioural situations in which vocalization occurs in *Proteles* visual signals are used at the same time. The aardwolf's agonistic sound repertoire is relatively diverse, including the wide-spread terrestrial carnivore sounds growling, snarling, and barking. According to the agitation of the sender, their intensity, and the likelyhood of ensuing aggressive action of the sender they can be arranged in the following ascending order: jaw click and lip smack → growl → snarl → bark. Thus, barks represent the most intense threat vocalization signalling that the sender is prepared to attack the addressee upon its further approach. Considering the very close functional proximity and the structural similarity of growls and snarls, the fact that one can easily change into the other and the fact that barks can arise from growling or snarling with hardly interrupting sound production it would be interesting to know the precise mechanisms of sound production in these vocalization types. However, we do not interpret barking as belonging to the graded system formed by growling and snarling because it clearly differs from these in structural characteristics, and vocalizations with intermediate structure did not occur.

We did not list hissing as an agonistic sound. It is present in the other extant families of the superfamily Feloidea, the felids (Wemmer and Scow 1977), viverrids (Wemmer 1977), and very probably also herpestids (Earlé 1981) as the phylogenetically closest relatives of the Hyaenidae (Hunt and Tedford 1993). However, this type of sound is also found in species of different families of the superfamily Arctoidea (sensu Wyss and Flynn 1993) as in the red panda (*Ailurus fulgens*) (Roberts and Gittleman 1984) or several *Mustela* species (Gossow 1970). Within longer recording stretches of snarling and growling in our aardwolf material there are a few short periods with low-intensity

exhalatory noise which may represent hissing. Our observations and the quality of these recordings are not good enough to make a definitive statement in this respect, though. Hissing was not listed as a vocalization type in any of the other species of the Hyaenidae (*Crocuta*: Kruuk 1972; Mills 1990; *Hyaena*: Kruuk 1976; *Parahyaena* Mills 1990) for which vocalization data were published and by any of the earlier publications dealing with acoustic communication in the aardwolf.

Further data are also necessary to establish the exact nature of "purring" in the aardwolf described here as compared to purring proper in the Viverridae (Wemmer 1977) and Felidae (Peters 1981; Frazer Sissom et al. 1991). Deane (1962) mentions a sound termed purring in the spotted hyaena. Based on the behavioural context given for this sound it is highly unlikely that it is equivalent to aardwolf "purring" or felid purring but its exact nature remains questionable.

So far neither jaw clicking nor lip smacking have been reported as acoustic threat signals in any species of the Hyaenidae, Felidae, Viverridae, or Herpestidae. If they function as genuine acoustic signals in *Proteles* they probably represent an autapomorphy of this species. The only other species of the Carnivora which are known to produce sounds by opening and closing of the jaws and lips during agonistic behaviour are in the family Ursidae (Jordan 1976), including the giant panda (*Ailuropoda melanoleuca*) (Peters 1985; Schaller et al. 1985) and the red panda (*Ailurus fulgens*) (Roberts and Gittleman 1984). The similarity of these sound signals between the aardwolf and the Ursidae is very likely to be explained by convergent evolution; the respective adaptive significance of these sounds in the two taxa and whether they evolved under equivalent functional constraints is open to question. Aardwolves lack any type of intense long range vocalization and the same seems to be true for the striped hyaena (Kruuk 1976) and the brown hyaena (Mills 1990). So, no other hyaenid species seems to have a vocalization type comparable to the whoop of the spotted hyaena (Kruuk 1972; Henschel 1986; Mills 1990). Mills (1990) mentions more vocalization types in the last species which may not be shared by any other species of the Hyaenidae.

All vocalizations of the aardwolf described in this study require better characterization in their typical structure, their range of variability and some of them possibly further differentiation on the basis of more recordings of appropriate quality and detailed behavioural observations. It is essential that the exact nature of the whizzing sound is established on the basis of sonagraphic analyses. Studies are desirable to check whether aardwolves have further vocalization types in addition to the ones described here. Because of the difficulties in observing and tape recording aardwolf acoustic communication in the field it seems appropriate to plan future studies into this topic with a mixed approach of observing wild and captive individuals.

Acknowledgements

A. S. would like to thank De Beer Consolitated Mines for permission to work on their property Benfontein Farm, as well as Mark and Tania Anderson to record sounds of their hand raised aardwolf 'Luna', and Philipp Richardson for various support and helpful discussion. His thanks go to Laura Freysen from the Transvaal Museum, Pretoria, for lending the sound recording equipment and the generous supply of tapes. This study was funded through a bursary from the German Academic Exchange Service (DAAD) and a research assistant bursary from the University of Pretoria to A. Sliwa. The McGregor Museum in Kimberley provided logistic support for him. Very helpful comments by Marion East, Heribert Hofer, Gus Mills, and Rainer Hutterer on an earlier version of the manuscript are gratefully acknowledged.

Zusammenfassung

Lautliche Kommunikation beim Erdwolf, Proteles cristatus (Carnivora: Hyaenidae).

Auf der Grundlage von Beobachtungen an freilebenden und in Menschenobhut gehaltenen Tieren und sonagraphischer Auswertung von Tonbandaufnahmen wird die lautliche Kommunikation juveniler und adulter Erdwölfe (*Proteles cristatus*) beschrieben. Zusätzlich zu den vorwiegend genutzten geruchlichen Signalen besitzen Erdwölfe eine Reihe von Lautäußerungen, die sie zur Verständigung mit Artgenossen über geringe bis mittlere Entfernung einsetzen. Eine spezifische Lautform zur Verständigung über größere Entfernungen (>500 m) ist nicht ausgebildet. Die Lautformen im Zusammenhang agonistischen Verhaltens sind am vielfältigsten. Von den bisher für die Art belegten 9 Lauttypen gehört ungefähr die Hälfte zu Lautkontinua, bei denen Übergänge zwischen einzelnen Typen auftreten. Bei den anderen handelt es sich wahrscheinlich um diskrete Typen. Es ist allerdings nicht gesichert, ob alle hier beschriebenen Lautformen des Erdwolfs wirklich zur akustischen Verständigung eingesetzt werden. Soweit dies anhand der bisher vorliegenden Beobachtungen zu beurteilen ist, unterscheidet sich das Lautrepertoire der Art deutlich von dem der anderen Arten der Hyaenidae.

References

Bartlett, J.; Bartlett, D. (1967): Nature's paradise. Boston: Houghton Mifflin.

Deane, N. N. (1962): The spotted hyaena, *Crocuta crocuta crocuta*. Lammergeyer **2**, 26–43.

Earlé, R. A. (1981): Aspects of social and feeding behaviour of the yellow mongoose, *Cynictis penicillata* (G. Cuvier). Mammalia **45**, 143–152.

East, M. L.; Hofer, H. (1991 a): Loud-calling in a female-dominated mammalian society. I. Structure and composition of whooping bouts of spotted hyaenas, *Crocuta crocuta*. Anim. Behav. **42**, 637–649.

East, M. L.; Hofer, H. (1991 b): Loud-calling in a female-dominated mammalian society: II. Behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. Anim. Behav. **42**, 651–669.

Estes, R. D. (1991): The behavior guide to African mammals. Berkeley: Univ. California Press.

Frazer Sissom, D. E.; Rice, D. A.; Peters, G. (1991): How cats purr. J. Zool. (London) **223**, 67–78.

Gossow, H. (1970): Vergleichende Verhaltensstudien an Marderartigen. I. Über Lautäußerungen und zum Beuteverhalten. Z. Tierpsychol. **27**, 405–480.

Henschel, J. R. (1986): The socio-ecology of a spotted hyaena (*Crocuta crocuta*) clan in the Kruger National Park. DSc dissertation, University of Pretoria.

Hunt, R. M., Jr.; Tedford, R. H. (1993): Phylogenetic relationships within the aeluroid Carnivora and implications of their temporal and geographic distribution. In: Mammal phylogeny. Placentals. Ed. by F. S. Szalay, M. J. Novacek, and M. C. McKenna. New York, Berlin: Springer-Verlag. Pp. 53–73.

Jordan, R. (1976): Threat behavior in the black bear (*Ursus americanus*). In: Bears – their biology and mangement. Ed. by M. Pelton, J. Lentfer, and G. Folk. Morges: IUCN Publ. no. 40. Pp. 57–63.

Kingdon, J. (1977): East African mammals. Vol. 3. Part A (Carnivores). London, New York: Academic Press.

Koehler, C. E.; Richardson, P. R. K. (1990): *Proteles cristatus*. Mammalian Species No. 363: 1–6. Lawrence, Kansas: American Soc. Mammalogists.

Kruuk, H. (1972): The spotted hyena: A study of predation and social behavior. Chicago: Univ. Chicago Press.

Kruuk, H. (1976): Feeding and social behaviour of the striped hyaena (*Hyaena vulgaris* Desmarest). E. Afr. Wildl. J. **14**, 91–111.

Kruuk, H.; Sands, W. A. (1972): The aardwolf (*Proteles cristatus* Sparrman 1783) as a predator of termites. E. Afr. Wildl. J. **10**, 211–227.

Mills, M. G. L. (1982): *Hyaena brunnea*. Mammalian Species No. 194: 1–5. Lawrence, Kansas: American Soc. Mammalogists.

Mills, M. G. L. (1990): Kalahari hyaenas. The comparative behavioural ecology of two species. London: Unwin Hyman.

Owens, D. D.; Owens, M. J. (1978): Feeding ecology and its influence on social organisation in brown hyaenas (*Hyaena brunnea*) in the central Kalahari desert. E. Afr. Wildl. J. **16**, 113–136.

Peters, G. (1981): Das Schnurren der Katzen (Felidae). Säugetierkdl. Mitt. **29**, 30–37.

Peters, G. (1984): On the structure of friendly close range vocalizations in terrestrial carnivores (Mammalia: Carnivora: Fissipedia). Z. Säugetierkunde **49**, 157–182.
Peters, G. (1985): A comparative survey of vocalization in the Giant panda (*Ailuropoda melanoleuca* David, 1869). Bongo **10**, 197–208.
Peters, G.; Wozencraft, W. C. (1989): Acoustic communication by fissiped carnivores. In: Carnivore behavior, ecology, and evolution. Ed. by J. L. Gittleman. Ithaka: Cornell Univ. Press. Pp. 14–56.
Richardson, P. R. K. (1985): The social behaviour and ecology of the aardwolf *Proteles cristatus* (Sparrman, 1783) in relation to its food resources. D.Phil. thesis, Oxford Univ.
Richardson, P. R. K. (1987): Aardwolf mating system: overt cuckoldry in an apparently monogamous mammal. S. Afr. J. Sci. **83**, 405–410.
Richardson, P. R. K. (1990): Scent marking and territoriality in the aardwolf *Proteles cristatus.* In: Chemical signals in vertebrates. Ed. by D. W. Macdonald, D. Müller-Schwarze, and S. E. Natynczuk. Oxford: Oxford Univ. Press. Pp. 378–387.
Richardson, P. R. K. (1991): Territorial significance of scent marking during the non-mating season in the aardwolf *Proteles cristatus* (Carnivora: Protelidae). Ethology **87**, 9–27.
Richardson, P. R. K.; Bearder, S. K. (1984): The hyena family. In: The encyclopaedia of mammals. Ed. by D. W. Macdonald. New York: Facts on File. Pp. 154–159.
Rieger, I. (1981): *Hyaena hyaena.* Mammalian Species No. 150: 1–5. Lawrence, Kansas: American Soc. Mammalogists.
Roberts, M. S.; Gittleman, J. L. (1984): *Ailurus fulgens.* Mammalian Species No. 222: 1–8. Lawrence, Kansas: American Soc. Mammalogists.
Schaller, G. B. (1972): The Serengeti lion. A study of predator-prey relations. Chicago: Univ. of Chicago Press.
Schaller, G. B.; Hu Jinchu; Pan Wenshi; Zhu Jing (1985): The Giant pandas of Wolong. Chicago: Univ. Chicago Press.
Scoville, R.; Gottlieb, G. (1978): The calculation of repetition rate in avian vocalizations. Anim. Behav. **26**, 962–963.
Shortridge, G. C. (1934): The mammals of South West Africa. London: Heinemann.
Skinner, J. D.; Smithers, R. H. N. (1990): The mammals of the southern African subregion. 2nd ed. Pretoria: Univ. Pretoria Press.
Sliwa, A. (1996): A functional analysis of scent marking and mating behaviour in the aardwolf, *Proteles cristatus* (Sparrman, 1783). Ph.D. thesis, University of Pretoria.
Smithers, R. H. N. (1971): The mammals of Botswana. Museum Memoir, Nat. Museums Rhodesia **4**, 1–340.
Smithers, R. H. N. (1983): The mammals of the southern African subregion. Pretoria: Univ. Pretoria Press.
Wemmer, C. M. (1977): Comparative ethology of the Large-spotted genet (*Genetta tigrina*) and some related viverrids. Smithson. Contr. Zool. No. **239**.
Wemmer, C. M.; Scow, K. (1977): Communication in the Felidae with emphasis on scent marking and contact patterns. In: How animals communicate. Ed. by T. A. Sebeok. Bloomington, London: Indiana Univ. Press. Pp. 749–766.
Wozencraft, W. C. (1993): Order Carnivora. In: Mammal species of the world. A taxonomic and geographic reference. 2nd ed. Ed. by D. E. Wilson and D. M. Reeder. Washington, D. C.: Smithsonian Institution Press. Pp. 279–348.
Wyss, A. R.; Flynn, J. J. (1993): A phylogenetic analysis and definition of the Carnivora. In: Mammal phylogeny. Placentals. Ed. by F. S. Szalay, M. J. Novacek, and M. C. McKenna. New York, Berlin: Springer-Verlag. Pp. 32–52.

Authors' addresses: Dr. Gustav Peters, Zoologisches Forschungsinstitut und Museum Alexander Koenig, Adenauerallee 160, D-53113 Bonn, Germany; Dr. Alexander Sliwa, Department of Zoology and Entomology, University of Pretoria, Pretoria, South Africa; presently: Hubertusallee 30, D-42117 Wuppertal, Germany

Z. Säugetierkunde **62** (1997) 239–249

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Blood protein variation in blackbuck (*Antilope cervicapra*), a lekking gazelle

By A. Schreiber, P. Fakler, and R. Østerballe

Zoologisches Institut der Universität Heidelberg, Heidelberg, Germany and Løveparken Zoo Givskud, Give, Denmark

Receipt of Ms. 02. 09. 1996
Accepture of Ms. 09. 02. 1997

Abstract

The electrophoretic screening of blood proteins representing products of 40 loci in 49 zoo-living blackbuck individuals (*Antilope cervicapra*) revealed polymorphism of transferrin, post-transferrin-2, and glucose phosphate isomerase-1, resulting in a percentage polymorphism of P = 0.075 (P = 0.034 for enzyme loci only), and an observed heterozygosity of H = 0.025 (H = 0.005 for enzymes only). These values suggest low protein polymorphism for *Antilope* when compared with most *Gazella* species. Inbreeding in captivity may explain this observation, or genetic drift in a lekking bovid with strong polygynous promiscuity. Apparently being a phylogenetic offshoot whose phenotype deviates markedly from an ancestral *Gazella*-like state chiefly in sexually selected characters, the tachytelic blackbuck lineage could have lost alleles since diverging from *Gazella*.

Introduction

The Indian blackbuck or sasin (*Antilope cervicapra*) is a gazelle (Antilopinae, Bovidae) inhabiting arid semideserts to mesic grasslands in India, Pakistan, and Nepal. Other than the controversial taxonomy of the approximately 16 species (and over 50 described taxa) in the central genus *Gazella* (e. g. Rostron 1972; Roberts 1977; Groves 1985, 1988; Furley et al. 1988; Vassart 1994), the systematic classification of blackbuck in a monotypic genus has not been contested until recently (Vassart 1994; Vassart et al. 1995 b). *Antilope* differs from *Gazella* by males having anticlockwise spiralled and rather inclined horns and conspicuous black coats sharply contrasting with their countershading white underparts; does are tawny or reddish-yellow (Haltenorth 1963; Roberts 1977). Compared with other bovid species, the relative length of horns of male blackbuck can reach remarkable dimensions when referenced to body height (Ranjitsinh 1989). Mainly to account for this sexual dimorphism, some taxonomists accepted tribus rank (Antilopini) to separate blackbuck from other gazelles. A characteristic translocation of the X-chromosome with one autosome, and many exclusive Robertsonian fusions are found in both blackbuck and *Gazella* as possible synapomorphies (Sharma et al. 1974; Effron et al. 1976; Gallagher and Womack 1992; Vassart et al. 1995 b). Osteology (Groves 1985) and allozyme data (Vassart 1994) were reported as a confirmation that blackbuck has descended from true gazelles (genus *Gazella*). The close relationship of sasin and gazelles is confirmed by successful hybridization even in free-ranging stocks: In the Gajner area (Bikaner, India), released male blackbuck were observed to court chinkara (*Gazella bennetti*) females; two viable female hybrids raised from a chinkara father and a sasin mother were sterile (Ranjitsinh 1989).

Blackbuck's close affinities with *Gazella* can hardly be doubted considering the available database, but the cladistics of their relationship remains unresolved. Effron et al. (1976) observed five putatively apomorphic chromosomal homologies uniting dama and Grant's gazelles (*Gazella dama* and *G. granti* of the subgenus *Nanger*) with *Antilope* to the reported exclusion of other *Gazella*-species. Vassart (1994) and Vassart et al. (1995 b) inferred from allozymes and chromosomal banding patterns either the clades comprising mountain (*G. gazella*) and dorcas gazelles (*G. dorcas*) or goitred (*G. subgutturosa*) and Cuvier's gazelles (*G. cuvieri*) as the most probable sister groups, and offered very robust bootstrap values in support of this inference. Morphological evidence confirms sasin's origin from a group of medium-sized gazelles, e. g. *G. dorcas*, *G. gazella*, Indian (*G. bennetti*) or Speke's (*G. speki*) gazelles (Vassart 1994). If one of these phylogenetic models is true, some species of *Gazella* should be more distantly related among each other than they are with *Antilope*, and blackbuck should have experienced accelerated evolution of its phenotype.

Blackbuck is the only gazelle in which arena display in lekking grounds has been observed, a system of mate choice where few dominant males monopolize reproduction (Ranjitsinh 1982, 1989). The resulting reproductive dominance of a limited number of males may diminish the genetic variation in populations and accelerate the fixation of phenotypic traits by sexual selection or genetic drift (Fisher 1930; Lande 1981). Despite the availability of models to quantitate the effect of male reproductive variance on genetic variation, few investigations attempted to correlate empirical molecular variability with mammalian mating systems (Apollonio and Hartl 1993; Sugg et al. 1996). The provision of blood samples from zoo-living blackbuck prompted us to compare protein variability in this polygynous ruminant with published data sets from several true gazelles to assess whether a gazelline with an untypical social system displays unusual population genetic patterns too.

Material and methods

Animals

This study is based on 49 blackbuck, i. e. 29 blackbuck kept at Givskud Zoo (Denmark), eleven from Cologne Zoo (Germany), five from Ålborg Zoo (Denmark), three from Rostock Zoo (Germany), and one from the Ménagerie du Jardin des Plantes, Paris (France). The herd at Givskud Zoo (previously kept at Copenhagen Zoo) descends from several imports to Copenhagen Zoo before 1950. Inbred over many years, an unrelated male was introduced in 1973 from Rotterdam Zoo, and a related male in 1974 from Ålborg Zoo. In 1993, the Givskud Zoo group was expanded by an unrelated breeding buck from Magdeburg Zoo. Sasin at Ålborg Zoo also descend from the Copenhagen lineage in the 1960s, but imports from Zürich Zoo (1983) and Artis Amsterdam (1993) were included. The Cologne group had been founded by animals obtained from Rotterdam and Munich Zoos, the sampled specimens being either imported individuals or their first-generation crosses. Blackbuck at Rostock Zoo descend from two male and one female founders from Berlin Zoo (1968), two males and seven females imported from India (1968), one pair from Djurpark Kolmarden, one male from Tierpark Hoyerswerda (1976), and two males and one female from Copenhagen Zoo (1979).

Blood sampling and electrophoresis

Blood samples (EDTA or acid citrate dextrose) were collected from the jugular vein, express-mailed to the laboratoy, and centrifugated immediately upon reception. Haemolysates and plasma were stored at –70 °C. Sonicated haemolysates were assayed in horizontal agarose gels, using the buffer conditions listed in table 1. Plasma proteins were resolved by PAGE in 12% polycrylamide resolution gels with 0.1% % N,N′-methylene-bis-acrylamide, 95 mM Tris and 13 mM citric acid (stacking gel: 4% acrylamide, 0.3% N,N′-methylene-bis-acrylamide, 190 mM Tris, 25 mM citric acid), using a discontinuous buffer sys-

tem (tray buffer: 66 mM Tris/32 mM boric acid pH 8.6), and visualized by staining in 0.06% Coomassie blue (in 40% methanol, 10% acetic acid, 50% aqua dest.). Prior to Coomassie-staining, PAGE-gels were assayed for plasma glutamate dehydrogenase. Zymogramme staining recipes followed HARRIS and HOPKINSON (1976).

Results

Allozymes and structural blood proteins representing the products of 40 genetic loci were resolved in up to 49 blackbuck from five zoological gardens. Thirty-seven loci were monomorphic, including haemoglobins, albumin, postalbumin-1, posttransferrin-1 and -3, plasma glutamate dehydrogenase, and nineteen erythrocyte allozymes representing 28 loci: Acid phosphatases (Acp-1*, Acp-2*), adenosine deaminase (Ada*), adenylate kinase (Ak-1*, Ak-2*), carbonic anhydrase (Ca*), NADH-diaphorase (Dia-1*, Dia-2*, Dia-3*), erythrocyte esterases (Es-1*, Es-2*, Es-3*, substrate: methyl-umbelliferyl acetate), glucose-6-phosphate dehydrogenase (G6pdh*), glucose phosphate isomerase (Gpi-2*), glutamate oxaloacetate transaminase (Got*), isocitrate dehydrogenase (Idh*), lactate dehydrogenases (Ldh-1*, Ldh-2*), malate dehydrogenases (Mdh*), unspecific dehydrogenase (1 Locus), malic enzyme (Me*), mannose phosphate isomerase (Mpi*), 6-phosphogluconate dehydrogenase (6-Pgd*), phosphoglucomutases (Pgm-1*, Pgm-2*), superoxide dismutases (Sod-1*, Sod-2*), nucleoside phosphorylase (Pnp*). Following the structural analysis by SHINDE and FURTADO (1981) who found two α-globin chains in each electrophoretic fraction of sasin haemoglobin, and a different β-chain in each of two bands into which blackbuck haemoglobin is resolved, we count the haemoglobin pattern as representing the products of four loci.

Two plasma proteins, transferrin (Tf) and posttransferrin-2 (Ptf-2) showed three phenotypes each in the 49 investigated blackbuck: The banding patterns at both loci segregated in all cases of known family genealogy like biallelic genetic polymorphisms. The Tf-system comprised a second, faster-migrating variant Tf*107 of 107% relative mobility when referenced to the main allele Tf*100. Tf bands were identified by comparing patterns with reference alleles from several other ruminant species. All three possible genotypes were present (Tf*100/100, Tf*100/107, Tf*107/107), their numbers did not deviate from Hardy-Weinberg distribution (Fig. 1). The functional identity of Ptf-2 remains unknown, but the designation “posttransferrin-2” refers to its electrophoretic migration as the second major plasma protein following transferrin cathodically. In addition to the more common allele Ptf-2*100, the second variant Ptf-2*83 reached 83% mobility. The combinations Ptf-2*100/100, Ptf 2*83/100, and Ptf-2*100 were observed in numbers corresponding to Hardy-Weinberg expectations (Fig. 1). Glucose phosphate isomerase (Gpi-1*) variation displayed the typical three-banded heterozygous zymogramme of a dimeric enzyme with the alleles Gpi-1*100 and Gpi-1*300: The intermediate band of heterozygotes representing the heterodimere Gpi-1*100/Gpi-1*300 yielded double enzyme activity when compared with both homodimeres, the cathodal Gpi-1*100/Gpi-1*100 and the anodal Gpi-1*300/Gpi-1*300 (Fig. 1). This distribution of enzyme activites can be expected because the four possible combinations of two alleles (100/100, 100/300, 300/100, 300/300) are electrophoretically resolved into only three bands, both heterodimeres coalescing into a common band representing 50% of overall enzyme activity (against 25% for each homodimere). This typical zymogramme was not encountered for the variant Gpi-1*600 whose heterozygotes with Gpi-1*100 indicated a much lower staining intensity of the anodal homodimere (Gpi-1*600/Gpi-1*600) than for the cathodal Gpi-1*100/Gpi-1*100 (Fig. 1). The heterodimere Gpi-1*100/Gpi-1*600, however, indicates approximately two-fold enzyme activity when compared with the Gpi-1*600-homodimere. We conclude that despite an unexpected distribution of staining intensities between bands, Gpi-1*600 is a valid allele able to enter heterodimeric combinations with the common variant. It may be

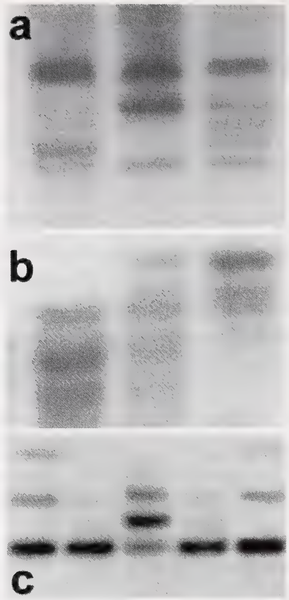


Fig. 1. Blackbuck (*Antilope cervicapra*). Three electrophorectic protein polymorphisms. 1 a. Posttransferrin-2 (Ptf-2*). Genotypes from left to right: Ptf-2* 100/100, Ptf-2* 83/83, Ptf-2* 83/100. 1 b. Transferrin (Tf*). Genotypes from left to right: Tf* 107/107, Tf* 107/100, Tf* 100/100. 1 c. Glucose phospate isomerase-1 (Gpi-1*). Genotypes from left to right: Gpi-1* 600/100, Gpi-1* 100/100, Gpi-1* 300/100, Gpi-1* 100/100, Gpi-1* 600/100. The negative pole is at the upper margin of micrographs 1 a and 1 b, and at the lower margin of micrograph 1 c.

either less strongly expressed and therefore be present in smaller quantities than the common allele, or this enzyme variant prefers biochemical conditions different to those supplied by our staining protocol, resulting in much weaker activities in our gels than would be expected for codominantly expressed alleles with a simple gene-dosage effect. As could be expected from allele frequencies, both Gpi-1*300 and Gpi-1*600 were confined to heterozygotes with Gpi-1*100; neither did we observe the genotype Gpi-1*300/600. Posttransferrin-1 produced variable patterns too, but the clear scoring of this system deteriorated with prolonged storage of frozen sera. Therefore, we neglect these variants until additional samples from pedigreed sasins are available to exclude non-genetic variability or storage artefacts.

Sample sizes, allele frequencies and heterozygosities of individual herds and of the combined metapopulation are listed in table 2. The fraction of polymorphic loci measured $P = 0.034$ for allozymes only, and $P = 0.075$ for enzymes and structural blood proteins. Heterozygosity was $H = 0.005$ for enzymes, and $H = 0.025$ for enzymes and serum proteins combined. These values are compared with published data on gazelle species listed in table 3.

Discussion

While Tf provides useful genetic marker alleles in several ruminants (SCHREIBER 1991), the homology and the function of post-transferrins remain unidentified. GAHNE et al. (1977) described a very similar polymorphism from domestic taurine cattle, also operationally

Table 1. Buffer systems used to resolve allozymes of blackbuck. Gel buffers are mostly prepared by diluting the respective electrode buffers (EB).

Enzyme	Electrode buffer	Gel buffer
Lactate dehydrogenase (E.C. 1.1.1.27)	100 mM NaOH/0.3 M boric acid, pH 8.6	67 mM Tris/5 mM NaOH/5 mM citric acid/15 mM boric acid, pH 8.6
Malate dehydrogenase (E.C. 1.1.1.37)	250 mM NaH_2PO_4/150 mM citric acid, pH 5.9 with NaOH	EB 1:40, pH 5.9
Malic enzyme (E.C. 1.1.1.40)	100 mM Tris, pH 7.4 with NaH_2PO_4	EB 1:10, pH 7.4
Isocitrate dehydrogenase (E.C. 1.1.1.42)	250 mM NaH_2PO_4/150 mM citric acid, pH 5,9 with NaOH	EB 1:40, pH 5,9
6-Phosphogluconate dehydrogenase (E.C. 1.1.1.44)	690 mM Tris/160 mM citric acid, pH 8.0 with HCl	EB 1:30, pH 8.0
Glucose-6-phosphate dehydrogenase (E.C. 1.1.1.49)	110 mM Tris/60 mM boric acid/ 2.5 mM EDTA, pH 8.6 with NaOH	EB 2:5, pH 8.6
NADH diaphorase (E.C. 1.6.2.2)	110 mM Tris/60 mM boric acid/ 2.5 mM EDTA, pH 8.6 with NaOH	EB 2:5, pH 8.6
Superoxide dismutase (E.C. 1.15.1.1)	250 mM NaH_2PO_4/150 mM citric acid, pH 5.9 with NaOH	EB 1:40, pH 5.9
Purine nucleoside phosphorylase (E.C. 2.4.2.1)	100 mM NaOH/0.3 M boric acid, pH 8.6	67 mM Tris/5 mM NaOH/5 mM citric acid/15 mM boric acid, pH 8.6
Glutamate oxaloacetate transaminase (E.C. 2.6.1.1)	200 mM NaH_2PO_4/150 mM Borat, pH 7.0	EB 1:10, pH 7.4
Adenylate kinase (E.C. 2.7.4.3)	200 mM Tris, pH 8.0 with citric acid	EB 1:3, pH 8.0
Phosphoglucomutase (E.C. 2.7.5.1)	100 mM Tris/100 mM maleic acid/ 10 mM $MgCl_2$/10 mM EDTA, pH 7.4	EB 1:10, pH 7.4
Esterases (E.C. 3.1.1.1)	100 mM Tris/100 mM maleic acid anhydride, pH 7.2	EB 1:10, pH 7.2
Acid phosphatase (E.C. 3.1.3.2)	150 mM trinatrium citrate/240 mM NaH_2PO_4, pH 6.3	EB 1:40, pH 6.3
Adenosine deaminase (E.C. 3.5.4.4)	110 mM Tris/60 mM boric acid/ 2.5 mM EDTA, pH 8.6 with NaOH	EB 2:5, pH 8.6
Carbonic anhydrase (E.C. 4.2.1.1)	110 mM Tris/60 mM boric acid/ 2.5 mM EDTA, pH 8.6 with NaOH	EB 2:5, pH 8.6
Glyoxalase (E.C. 4.4.1.5)	200 mM Tris/HCl, pH 8.0	EB 1:10, pH 8.0
Mannose phosphate isomerase (E.C. 5.3.1.8)	100 mM Na_2HPO_4/100 mM NaH_2PO_4, pH 7.0	EB 1:10, pH 7.0
Glucose phosphate isomerase (E.C. 5.3.1.9)	250 mM Tris/60 mM citric acid, pH 7.5	60 mM Tris/2 mM citric acid, pH 7.5

called Ptf-2. There was no deviation from the expected family segregation in the known segments of the sasin pedigree, and both Ptf-2 variants certainly represent Mendelian alleles. Both polymorphic serum proteins and one triallelic isoenzyme may be useful markers for the genetic management of blackbuck populations. Gazelles are a group of ruminants whose management poses problems in both zoos and nature reserves by documented inbreeding depression (Templeton and Read 1984; Templeton et al. 1987) and controversial taxon definition (Granjon et al. 1991; Bigalke et al. 1993; Vassart 1994); different con-

Table 2. Protein polymorphism in captive-bred blackbuck. n = sample size; p_x, p_y, p_z = allele frequencies; H = observed heterozygosities (H_o) and their Hardy-Weinberg expectations (H_e).

		Tf			Ptf-2			Gpi-1*			
	n	p_{100}	p_{107}	H_o/H_e	p_{100}	p_{83}	H_o/H_e	p_{100}	p_{300}	p_{600}	H_o/H_e
total	49	0.774	0.226	0.340/0.354	0.565	0.435	0.500/0.496	0.918	0.072	0.010	0.163/0.152
Givskud	29	0.776	0.224	0.310/0.354	0.483	0.517	0.552/0.508	0.983	0.017	0.000	0.034/0.033
Cologne	11	0.773	0.227	0.455/0.368	0.636	0.364	0.545/0.485	0.864	0.136	0.000	0.273/0.267
Alborg	5	0.900	0.100	0.200/0.180	0.800	0.200	0.400/0.320	0.900	0.000	0.100	0.200/0.180
Rostock	3	0.500	0.500	1.000/0.500	1.000	0.000	–	0.500	0.500	0.000	1.000/0.500
Paris	1	1.000	0.000	–	0.000	1.000	–	1.000	0.000	0.000	–

Table 3. Variabillity of protein electromorphs in various gazelles. P = fraction of polymorphic loci. H = percentage of heterozygous patterns (for springbok and blackbuck, the expected heterozygosity is provided, calculated on the basis of allele frequencies, the other studies indicate values of observed heterozygosity). n. s. = not specified.

Species	Sample size	Loci	*P*	*H*	Authors
Thomson's gazelle					
Gazella thomsoni	33	40	0.196	0.055	Georgiadis et al. (1990)
Gazella thomsoni albonotata	8	16	0.187	0.085	Vassart et al. (1994)
dorcas gazelle					
Gazella dorcas	25	16	0.187	0.074	Vassart et al. (1994)
Springbok					
Antidorcas marsupialis	24	46	0.174	0.060	Bigalke et al. (1993)
Speke's gazelle	27	19[1]	0.158[1]	n. s.	Templeton et al. (1987)
Gazella spekei		28[2]	0.143[2]		
goitred gazelle					
G. subgutturosa marica	30	16	0.125	0.021	Vassart et al. (1994)
	30	20	0.150	0.017	Granjon et al. (1991)
mountain gazelle					
G. g. gazella	16	16	0.062	0.027	Vassart et al. (1994)
	14	24	0.167	0.050	Vassart et al. (1995 a)
G. g. cora	7	16	0.062	0.008	Vassart et al. (1994)
	2	24	0.208	0.088	Vassart et al. (1995 a)
G. g. farasani	5	16	0.062	0.030	Vassart et al. (1994)
G. g. erlangeri	15	16	0.000	0.000	Vassart et al. (1994)
	2	24	0.000	0.000	Vassart et al. (1995 a)
blackbuck	49	29[1]	0.034[1]	0.005[1]	this study
Antilope cervicapra	49	40[2]	0.075[2]	0.025[2]	

[1] = isoenzyme loci
[2] = isoenzymes, haemoglobins and plasma proteins

cepts are available on sasin microtaxomomy (Zukowsky 1927, 1928; Groves 1982). An inhabitant of open grassy plains, sasin initially profited from human agriculture clearing dry forests, and historic concentrations of 10 000 specimens, or more, have been observed on single cattle ranches (Jerdon 1874). Total population estimates from the past are unreliable but an Indian nobleman alone kept 1 000 tame cheetahs chiefly for blackbuck hunting (Ranjitsinh 1989). Centennial reductions left only 43 500 blackbuck for India in 1989, scattered over numerous, isolated and generally rather small herds (Ranjitsinh 1989). Feral stocks in Texas and Argentina number a couple of thousands, they are used, together with zoo-bred sasin, to repopulate extirpated herds in Pakistan (Ranjitsinh 1989). This conservation management would profit from more extensive knowledge of population variability and differentiation to select proper herds for restocking.

Compared with other Antilopinae, blackbuck proteins proved fairly homozygous. Even when Tf and Ptf-2 are considered, loci which have been studied only rarely by previous investigators of gazelline polymorphism, sasins range at the lower end of previously observed allelic diversities. Small samples from captive mountain gazelles (*G. gazella*) showed similar or lower variability at 16 loci but VASSART et al. (1995 a) raised the documented variability of two subspecies of *G. gazella* when increasing the number of sampled loci from 16 to 24. Small specimen and locus samples easily distort allele frequencies, and differences in electrophoretic methods might influence the comparison of allozyme data too. Still, the available evidence proposes that blackbuck contains less genetic variation as a species than do most true gazelles. As an alternative, continued captive breeding has eroded the genetic variation from a previously more polymorphic state. We cannot decide this alternative with certainty without including samples from wild populations, but relevant arguments are summarized.

Kept in large groups, many blackbuck are unknown to zoo curators as individuals, and studbook management is absent. Captive-bred for the first time in 1888 (SCHWARZ 1980), the origins of modern herds predates the time when detailed records were documented in zoological gardens. Therefore, we are ignorant of many details of the breeding history. There are exceptions like Tierpark Berlin which has bred 250 blackbuck from up to nine male and 12 female founders by 1995 (POHLE 1995), and the Rostock Zoo herd whose history is also fairly well documented (SCHWARZ 1980; K. LINKE, pers. comm.). Hamadryas baboon (*Papio hamadryas*), another traditional zoo species in which few dominant males reproduce in any colony, revealed allozyme polymorphism and heterozygosity reduced by possibly 75% and 80% respectively, after 30 years of captive breeding without a studbook (WANG and SCHREIBER 1996). Different to baboons (WANG and SCHREIBER 1996), allele frequencies which would indicate genetic drift between zoo stocks were not observed in blackbuck. The stocks at the zoos of Cologne, Givskud, and Rostock had seen the import of unrelated individuals prior to sampling. Founder effects when establishing the zoo population decades ago might also have been moderate because representatives of both blackbuck subspecies (GROVES 1982) may be discerned among current zoo phenotypes. *A. c. rajputanae* from northwest India and formerly Pakistan have larger skulls, the sable-coated males have a grey sheen, rough long hair, and broad white rings surround the eyes; *A. c. cervicapra* from central-south India has shorter skulls, a narrow eye-ring, and shorter fine hair (GROVES 1982). Based on some 100 blackbuck imported into European zoos in the 1920 s, ZUKOWSKY (1927, 1928) described four different species. This splitting attitude has been reconciled with modern taxonomy by GROVES (1982) who lumped these species into two subspecies, but from the geographic information and the accompanying photographs by ZUKOWSKY (1927, 1928) one may conclude that sasins from all over India have entered the European zoo population. The smaller type with weakly divergent, open-spiralled shortish horns prevails in contemporary zoo herds, but blackbuck matching the phenotypes of northern populations are also included in our sample which includes descendants from at least twelve zoo herds. Since zoos chiefly exchanged breeding males, many more captive-bred sasin are cross-bred between lineages than is superficially indicated by the numbers of import of unrelated individuals. Moreover, the other published studies of electrophoretic variation in gazelles listed in table 3 also refer to captive specimens with a single exception (BIGALKE et al. 1993), and sometimes to inbred stocks indeed (TEMPLETON and READ 1984; TEMPLETON et al. 1987).

RANJITSINH (1982, 1989) described lekking in Velavadar National Park (NW India), where 1 300–1 700 sasin occur at a density of one per hectare (RASHID 1978; JHALA et al. 1992): 48–52 adult male sasins crowded on a display ground of 680 × 430 square metres, with a core area of 385 × 290 square metres comprising 30 territories. Microterritories in the sasin arena are advertised by postures and motions of the black-and-white bucks, and by pellet heaps in their centres on which bucks may sit down (RANJITSINH 1989). Lekking

implies the occupation of periodically established display territories where males aggregate solely for course of the rutting season, the most dominant buck typically conquering privileged sites which are preferred by mate-seeking females. Lekking behaviour is sufficiently common and conspicuous in sasin for Gujarati people to use a particular designation for small lek territories, *akhlis* (Ranjitsinh 1982). Lekking was also observed in Chapar Tal Sanctuary, Ratjastan (Ranjitsinh 1989) and at Guleria, Nepal (Bauer and Ellenberg 1993) but appears to be inconspicuous elsewhere (Schaller 1967; Meier et al. 1973; Lehmkuhl 1981; Bharucha and Asher 1993; Bauer and Ellenberg 1993). Lehmkuhl (1981) and Bauer and Ellenberg (1993) suggested that reproductive behaviour of sasin was density-correlated, that lekking may be confined to aggregations in good habitats, and that male monopolized stable female breeding groups when population density was low. Observers of zoo-living or feral blackbuck restrained in enclosures expectedly did not encounter leks, but agree on polygynous sociology and mating competition (Meier et al. 1973; Dubost and Feer 1981; Mungall 1991). Ranjitsinh (1989) observed the longest horns and darkest pelage in dominant males with successful access to receptive females. The display of black coats in open sun-dry semideserts (at temperatures rising to 48 °C in the shade) must confer physiological stress by heat absorption and water deprivation (Jhala et al. 1992), a disadvantage which appears to be outweighted by sexual selection (Ranjitsinh 1989). Polygynous promiscuity is detrimental to the preservation of population polymorphism because many males are excluded from siring offspring.

Fisher (1930) and Lande (1981) developed a model of "run-away-evolution" for species with strong sexual selection by females on male polygenic traits. Such species would evolve sexual dimorphism in signalling characters. Distorted contribution to reproduction by few males fulfilling female selection criteria would result in small genetically effective population sizes narrowing variability. Ultimately, frequent speciation events result from small changes in criteria of female choice in certain populations. There are only few prerequisites to fulfil this model of "runaway evolution", e. g. genetic linkage of inborn female selection criteria for particular male phenotypes with the loci determining those male appearances. The length and form of sasin horns appear to vary on a local rather than on a macrogeographic scale, but there is a tendency for the longest, most divergent, and most closely spiralled horns to occur in males of the subspecies *A. c. rajputanae* which inhabits the region where lekking populations have been identified (Groves 1982; Ranjitsinh 1989). Twenty-one of the 24 top hunting trophies harvested from sasin originated from the area occupied by this population (Ranjitsinh 1989). The model by Lande (1981) predicts a speciose clade of genetically rather monomorphic taxa. Fossil spiral-horned gazelles resembling blackbuck in horn form, dentition or crania are known from Pliocene and Pleistocene deposits, i. e. *Helicotragus*, *Palaeoreas*, *Protragelaphus*, *Antilospira*, *Gazellospira*, *Spirocerus*, *Prostepsiceros*, and *Antilope subtorta* (Pilgrim and Schaub 1939; Thenius 1969; Gentry 1970, 1971, 1976). This diversity of fossil spiral-horned genera which may or may not reside in sasin's ancestry could corroborate the rapid typogenesis predicted by the Lande (1981) model. As a contrast to the vivid speciation in spiral-horned gazelles, Miocene fossils from Europe and North Africa testify to the greater age and temporal continuity of *Gazella*, the inferred paraphyletic genus from which blackbuck appears to have descended (Effron et al. 1976; Vassart 1994; Vassart et al. 1995 b).

Correlations between biochemical polymorphism and lifestyle cannot prove causal connections. Field work on sasin sociology and large-scale population genetic inventories of free-living local populations, both lekking and non-lekking, are needed to confirm that the models of Fisher (1930) and Lande (1981) provide an explanation for the microevolution of blackbuck. However, in a period when decisions are required of how to manage the genetic variability of disappearing wildlife, the possible correlation between mating system (or other life-history traits) and allelic variability calls for cautious interpretation when finding high or low levels of allelic variability in studbook populations of relict

stocks (SUGG et al. 1996). Conservation breeding plans would profit from a better knowledge of genetically effective population sizes to estimate the level of inbreeding which is typical of free-living blackbuck populations.

Acknowledgement

We gratefully acknowledge the provision of blood samples by Drs. J.-L. BERTHIER (Ménagerie du Jardin des Plantes, Paris), K. LINKE (Zoo Rostock) and W. ZIMMERMANN (Zoo Köln). K. LINKE kindly recherched the breeding history of sasins at Rostock Zoo.

Zusammenfassung

Niedrige Allozym-Heterozygotie in Hirschziegenantilopen aus Zoologischen Gärten

Die elektrophoretische Analyse von 40 Blutproteinen bei 49 zoolebenden Hirschziegenantilopen (*Antilope cervicapra*) erbrachte die für Gazellen niedrigen Werte von P = 0.075 (P = 0.025 nur für Enzymloci) für den Anteil polymorpher Loci und H = 0.034 (H = 0.005 für Allozyme) für die beobachtete Heterozygotie. In Ermangelung von Vergleichsproben aus Freilandbeständen kann ein varianzmindernder Einfluß der Zucht in Gefangenschaft nicht ausgeschlossen werden. Jedoch sprechen paläontologische Befunde (rasche Typenbildung) ebenso wie der für eine Gazelle außergewöhnliche Sexualdimorphismus und das bei Antilopinae einzigartige Sozialsystem (Arenabalz) dafür, daß die Hirschziegenantilope einer raschen Mikroevolution unterliegen sollte. Geringe genetische Effektivpopulationen, verbunden mit sexueller Auslese, wären Faktoren der arteigenen Lebensweise, welche die genetische Variabilität absenken.

References

APOLLONIO, M.; HARTL, G. B. (1993): Are biochemical-genetic variation and mating systems related in large mammals? Acta Theriol. **38**, Suppl. 2, 175–185.

BAUER, J. J.; ELLENBERG, H. (1993): Status and management of blackbuck (*Antilope cervicapra rupicapra*) in Nepal – with observations on behaviour and factors affecting its population size. Tigerpaper **20**, 1–11.

BHARUCHA, E.; ASHER, K. (1993): Behaviour patterns of the blackbuck *Antilope cervicapra* under suboptimal habitat conditions. J. Bombay Nat. Hist. Soc. **90**, 371–395.

BIGALKE, R. C.; HARTL, G. B.; BERRY, M. P. S.; HENSBERGEN, J. VAN (1993): Population genetics of the springbok *Antidorcas marsupialis* – a preliminary study. Acta Theriol. **38**, Suppl. 2, 103–111.

DUBOST, G.; FEER, F. (1981): The behaviour of the male *Antilope cervicapra* L., its development according to age and social rank. Behaviour **76**, 62–127.

EFFRON, M.; BOGART, M. H.; KUMAMOTO, A. T.; BENIRSCHKE, K. (1976): Chromosome studies in the mammalian subfamily Antilopinae. Genetica **46**, 419–444.

FISHER, R. A. (1930): The genetical theory of natural selection. Oxford: Clarendon Press.

FURLEY, C. W.; TICHY, H.; UERPMANN, H.-P. (1988): Systematics and chromosomes of the Indian gazelle, *Gazella bennetti* (Sykes, 1831). Z. Säugetierkunde **53**, 48–54.

GAHNE, B.; JUNEJA, R. K.; GROLMUS, J. (1977): Horizontal polyacrylamide gradient gel electrophoresis for the simultaneous phenotyping of transferrin, post-transferrin, albumin and post-albumin in the blood plasma of cattle. Anim. Blood Groups biochem. Genet. **8**, 127–137.

GALLAGHER, D. S.; WOMACK, J. E. (1992): Chromosome conservation in the Bovidae. J. Hered. **83**, 287–298.

GENTRY, A. W. (1970): The Bovidae (Mammalia) of the Fort Ternan fossil fauna. In: Fossil vertebrates of Africa. II. Ed. by L. S. B. LEAKEY and R. J. G. SAVAGE. New York: Acad. Press. Pp. 243–323.

GENTRY, A. W. (1971): The earliest goats and other antelopes from the Samos *Hipparion* fauna. Bull. Brit. Mus. (Nat. Hist.) Geol. **20**, 231–296.

GENTRY, A. W. (1976): Bovidae of the Omo deposits. In: Earliest man and environments in the Lake Rudolf Basin. Ed. by Y. COPPENS, F. C. HOWELL, G. L. ISAAC, and R. E. F. LEAKEY. Chicago: University Press. Pp. 275–292.

Gentry, A. W. (1992): The subfamilies and tribes of the family Bovidae. Mammal. Rev. **22**, 1–32.
Georgiadis, N. J.; Kat, P. W.; Oketch, H.; Patton, J. (1990): Allozyme divergence within the Bovidae. Evolution **44**, 2135–2149.
Granjon, L.; Vassart, M.; Greth, A.; Cribiu, E.-P. (1991): Genetic study of sand gazelles (*Gazella subgutturosa marica*) from Saudi Arabia. Z. Säugetierkunde **56**, 169–176.
Groves, C. P. (1982): A note on geographic variation in the Indian blackbuck (*Antilope cervicapra* Linnaeus, 1758). Rec. zool. Surv. India **79**, 489–503.
Groves, C. P. (1985): An introduction to the gazelles. Chinkara **1**, 4–16.
Groves, C. P. (1988): A catalogue of the genus *Gazella*. In: Conservation and biology of desert antelopes. Ed. by A. Dixon and D. Jones. London: C. Helm. Pp. 193–198.
Haltenorth, Th. (1963): Klassifikation der Säugetiere: Artiodactyla. Handbuch der Zoologie **VIII**, Teil 1 (18), 1–167.
Harris, H.; Hopkinson, D. A. (1976): Handbook of enzyme electrophoresis in human genetics. Amsterdam–Oxford: North-Holland Publ. Comp.
Jerdon, T. C. (1874): The mammals of India. London: John Wheldon.
Jhala, Y. V.; Giles, R. H.; Bhagwat, A. M. (1992): Water in the ecophysiology of blackbuck. J. Arid Environments **22**, 261–269.
Lande, R. (1981): Models of speciation by sexual selection on polygenic traits. Proc. Natl. Acad. Sci., U.S.A. **78**, 3721–3725.
Lehmkul, J. F. (1981): Some aspects of the life history of blackbuck in Nepal. J. Bombay Nat. Hist. Soc. **77**, 444–449.
Meier, E.; Anderegg, R.; Kleiber, H.; Leimbacher, R.; Sommer, E.; Welti, W. (1973): Zum Sozialverhalten der Sasin oder Hirschziegenantilope (*Antilope cervicapra* L.). Vierteljahresschrift naturforsch. Ges. Zürich **118**, 107–128.
Mungall, E. C. (1991): Establishment of lying out: an example for blackbuck (*Antilope cervicapra*). Appl. Anim. Behav. Sci. **29**, 15–37.
Pilgrim, G. E.; Schaub, S. (1939): Die schraubenhörnige Antilope des europäischen Oberpliocaens und ihre systematische Stellung. Abh. Schweiz. Palaeontol. Ges. **62**, 1–30.
Pohle, C. (1995): Nilgau (*Boselaphus tragocamelus*) und Hirschziegenantilope (*Antilope cervicapra*) im Tierpark Berlin-Friedrichsfelde. Milu (Berlin) **8**, 629–634.
Ranjitsinh, M. K. (1982): Territorial behaviour of the Indian blackbuck (*Antilope cervicapra* Linnaeus, 1758) in the Velavadar National Park, Gujarat. J. Bombay Nat. Hist. Soc. **79**, 241–246.
Ranjitsinh, M. K. (1989): The Indian blackbuck. Dehradun: Natraj Publishers.
Rashid, M. A. (1978): Census of blackbucks in the Velavadar National Park of Gujarat State. J. Bombay Nat. Hist. Soc. **75**, 479–482.
Roberts, T. J. (1977): The mammals of Pakistan. London, Tonbridge: Ernest Benn.
Rostron, J. (1972): A multivariate statistical study of skull measurements of five taxa of gazelles. Biol. J. Linn. Soc. **4**, 1–14.
Schaller, G. B. (1967): The deer and the tiger. A study of wildlife in India. Chicago: Univ. Press.
Schreiber, A. (1991): Molekulare Individualität und Naturschutz. Populationsgenetische Beiträge zur Erhaltung bedrohter Arten. Diss., University of Heidelberg.
Schwarz, D. (1980): Haltung und Entwicklung der Hirschziegenantilopengruppe oder Sasingruppe (*Antilope cervicapra* L., 1758) im Zoologischen Garten Rostock. Zool. Garten N.F. **50**, 317–320.
Sharma, G. P.; Sobti, R. C.; Khattar, N. (1974): Karyometric analysis and its significance in *Antilope cervicapra*. Res. Bull. Panjab Univ. **25**, 17–20.
Shinde, R.; Furtado, M. (1981): Probable gene duplication in α-chain locus of the blackbuck *Antilope cervicapra*. Ind. J. Exp. Biol. **19**, 1197–1198.
Sugg, W.; Chesser, R. K.; Dobson, F. S.; Hoggland, J. L. (1996) Population genetics meets behavioural ecology. Trends Ecology Evolution **11**, 338–342.
Templeton, A. R.; Read, B. (1984): Factors eliminating inbreeding depression in a captive herd of Speke's gazelle (*Gazella spekei*). Zoo Biology **3**, 177–199.
Templeton, A. R.; Davis, S. K.; Read, B. (1987): Genetic variability in a captive herd of Speke's gazelle (*Gazella spekei*). Zoo Biology **6**, 305–313.
Thenius, E. (1969): Stammesgeschichte der Säugetiere (Einschließlich der Hominiden). Handbuch der Zoologie, **8**. Band, 2. Teil.
Vassart, M. (1994): Évolution et diversité génétique chez les gazelles (*Gazella*); apports de l'électrophorèse des protéines, de la cytogénétique et des microsatellites. Diss., University Paris-Sud.

Vassart, M.; Granjon, L.; Greth, A.; Catzeflis, F. M. (1994): Genetic relationships of some *Gazella* species: an allozyme survey. Z. Säugetierkunde **59**, 236–245.

Vassart, M.; Granjon, L.; Greth, A. (1995 a): Genetic study of *Gazella gazella*: chromosomal and allozymic data. C.R. Acad. Sci. Paris, Sciences de la Vie **318**, 27–33.

Vassart, M.; Séguéla, A.; Hayes, H. (1995 b): Chromosomal evolution in gazelles. J. Hered. **86**, 216–227.

Wang, M.; Schreiber, A. (1996): Low blood protein heterozygosity in zoo-bred hamadryas baboons. Comp. Biochem. Physiol. **113 B**, 403–409.

Zukowsky, L. (1927): Bemerkungen über die rassenweise Verschiedenheit der Hirschziegenantilope. Carl Hagenbecks Illustr. Tier- und Menschenwelt **2**, 124–127.

Zukowski, L. (1928): Weitere Mitteilungen über die Systematik der Hirschziegenantilope. Carl Hagenbecks Illustr. Tier- und Menschenwelt **3**, 60–62.

Authors' addresses: Dr. Arnd Schreiber, Dipl.-Biol. Peter Fakler, Zoologisches Institut der Universität Heidelberg, Im Neuenheimer Feld 230, D-69120 Heidelberg; Dr. Richard Østerballe, Løveparken Givskud, Give, Denmark

Z. Säugetierkunde **62** (1997) 250–252

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNGEN

Erstnachweis der Brandmaus (*Apodemus agrarius*) für Österreich. Mammalia austriaca 22

First record of the Field mouse (*Apodemus agrarius*) in Austria.

Von Friederike Spitzenberger

Naturhistorisches Museum Wien, Wien, Österreich

Eingang des Ms. 18. 11. 1996
Annahme des Ms. 17. 02. 1997

Am 14. 10. 1996 wurden an zwei S und SSE von Sicheldorf, Gemeinde Radkersburg, Steiermark gelegenen Fundstellen (46°40′ N/16°01′ E und 46°40′ N/16°02′E) in 200 m Seehöhe sechs Brandmäuse (*Apodemus agrarius*) gefangen. Sie stellen den Erstnachweis dieser Art für Österreich dar.

Bauer (1960) stellte die bis dahin publizierten Falschmeldungen von *A. agrarius* für Österreich zusammen und prophezeite völlig richtig, daß die Art, wenn überhaupt in Österreich, in den feuchten und warmen Niederungen des Südburgenlandes oder der Südsteiermark zu finden sein würde. Ein Fangversuch vom 3.–8. September 1962 bei Sicheldorf und Bad Radkersburg in für die Brandmaus geeigneten Habitaten (630 Fallennächte, die 93 Kleinsäuger in 10 Arten erbrachten) führte allerdings ebensowenig zum Nachweis von *A. agrarius* wie die Analyse von 1963 in Bad Radkersburg gesammelten Schleiereulengewöllen, die 2 000 Beutetiere mit 17 Säugetierarten umfaßte.

Nach der Publikation Bauers (1960) wurde *A. agrarius* noch zweimal, allerdings fälschlich, für Österreich angegeben. Kahmann (1961) glaubte sich zu erinnern, die Brandmaus 1938 im Leithagebirge gesammelt zu haben, doch liegt wohl eine Verwechslung vor, und Belege fehlen. Ein Vorkommen im Leithagebirge wäre außerdem sehr weit vom nächsten damals bekannten Fundort in Türje, Ungarn (Vásárhelyi 1939) entfernt gewesen. Heute kann das Leithagebirge als so gut durchforscht gelten, daß das Vorhandensein der Brandmaus hier ausgeschlossen werden kann. Schmidt und Topál (1976) bestätigten zwar das Fehlen der Art im Neusiedlerseegebiet für den ungarischen Teil, mißdeuteten aber Bauers (1960) Text als Hinweis auf ein Vorkommen im österreichischen Teil.

Die beiden nah benachbarten österreichischen Fundorte liegen im äußersten Südosten Österreichs im Zwickel zwischen der Mur und ihrem nördlichen Zufluß Kutschenitza, der knapp jenseits der österreichischen Grenze in Slowenien in die Mur mündet (1, 2 – Abb. 1). Das Vorkommen schließt damit direkt an die slowenischen Fundorte Radenci (3 – Hille und Meinig 1996), Turjanci (4 – Kryštufek 1991), Bunčani (5) und Ljutomer (6 – Kryštufek 1985) südlich der Mur, Dolnja Bistrica (7), Lendava (8) und Murska šuma (9 – Kryštufek 1985) nördlich der Mur an.

Die beiden österreichischen Fundstellen liegen im Bereich der ehemals ausgedehnten Auwälder der Mur und ihrer Nebengewässer im illyrischen Klimabereich, der durch warme, feuchte Sommer gekennzeichnet ist. Heute präsentiert sich die Landschaft als kleinräumiges Mosaik bestehend aus degradiertem Erlen-Eschenauwald, der in Parzellen geringer Größe gegliedert ist, und ausgedehnten Maisfeldern, die an die Stelle der ehema-

Abb. 1. Nachweise der Brandmaus (*Apodemus agrarius*) in Österreich (Punkte) und im angrenzenden Teil Sloweniens (Ringe). Erklärungen im Text.

ligen Wiesen, von denen heute nur geringe Reste vorhanden sind, getreten sind. Die Brandmäuse wurden an mit Goldrute, Brennessel und Brombeere verkrauteten Waldrändern zu grasbewachsenen Wegen und Wiesen und in einem trockengefallenen Saumgang der Mur (Lahn), der dicht mit Goldrute, Brennessel und anderen Hochstauden bestanden ist, gefangen. Dieser Habitat entspricht in allen Merkmalen demjenigen, der auch in der auf umfangreichen Untersuchungen fußenden Studie der Autökologie von *A. agrarius* in Mitteleuropa als optimal erkannt wurde (Zejda 1967).

Die Frage, seit wann *A. agrarius* seine Verbreitung auf österreichisches Staatsgebiet ausgedehnt hat, muß naturgemäß unbeantwortet bleiben. Es ist jedenfalls bekannt, daß der nördliche Rand des südlichen Areals dieser Art dynamisch ist. Görner (1976) und Pelikán (1989) nehmen an, daß in Zeiten lokaler Massenvermehrungen (Zejda 1967) das Areal ausgedehnt werden kann. Für eine Einwanderung nach Österreich in jüngster Zeit spricht die Tatsache, daß sie Bauer trotz intensiver Nachsuche in den Jahren 1962–63 hier nicht feststellen konnte.

Danksagung

Ich danke Dr. Kurt Bauer für die Zusammenstellung seiner auf den Nachweis der Brandmaus gerichteten Untersuchungen.

Literatur

Bauer, K. (1960): Die Säugetiere des Neusiedlersee-Gebietes. Bonn. zool. Beitr. **1**, 141–344.

Görner, M. (1976): Zum Vorkommen und zur Verbreitung der Brandmaus (*Apodemus agrarius*) in der DDR. In: Westareal der Verbreitung der Brandmaus (*Apodemus agrarius* (Pallas, 1778)). Ed. by J. Krachtovíl. Act. sci. nat. Brno **10**, 57–64.

HILLE, A.; MEINIG, H. (1996): The subspecific status of European populations of the striped field mouse *Apodemus agrarius* (Pallas, 1771) based on morphological and biochemical characters. Bonn. zool. Beitr. **46**, 203–231.

KAHMANN, H. (1961): Beiträge zur Säugetierkunde der Türkei 2. Die Brandmaus (*Apodemus agrarius* Pallas, 1774) in Thrakien und die südeuropäische Verbreitung der Art. Istanbul Üniv. Fen Mecm. Ser. B **26**, 87–106.

KRYŠTUFEK, B. (1985): Variability of *Apodemus agrarius* (Pallas, 1771) (Rodentia, Mammalia) in Yugoslavia and some data on its distribution in the northwestern part of the country. Biol. Vestn. **33**, 27–40.

KRYŠTUFEK, B. (1991): Sesalci Slovenije. Ljubljana, Prirodoslovni muzej Slovenije.

PELIKÁN, J. (1989): Mysice temnopásá *Apodemus agrarius* (Pallas, 1771) v jihlomoravkem kraji. Lynx (Praha) n. s. **25**, 106–108.

SCHMIDT, E.; TOPÁL, G. (1976): Die Verbreitung der Brandmaus (*Apodemus agrarius*) in Ungarn. In: Westareal der Verbreitung der Brandmaus (*Apodemus agrarius* (Pallas, 1778)). Ed. by J. KRATOCHVÍL. Act. sci. nat. Brno **10**, 21–26.

VÁSÁRHELYI, I. (1939): Beiträge zur Kenntnis der Säugetier-Fauna Ungarns. II. Fragm. Faun. Hung. **2**, 53–54.

ZEJDA, J. (1967): Habitat selection in *Apodemus agrarius* (Pallas, 1778) (Mammalia: Muridae) on the border of the area of its distribution. Zool. listy **16**, 15–30.

Anschrift d. Verf.: Dr. FRIEDERIKE SPITZENBERGER, Naturhistorisches Museum Wien, Postfach 417, A-1014 Wien, Österreich

Z. Säugetierkunde **62** (1997) 253–254

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Evidence for aboveground activity of Zambian Molerats (*Cryptomys*, Bathyergidae, Rodentia)

By A. Scharff and O. Grütjen

Abt. Allgemeine Zoologie, Universität-GH Essen, Essen

Receipt of Ms. 29. 11. 1996
Acceptance of Ms. 09. 02. 1997

By definition, subterranean mammals spend most of their lives in underground burrows, where they find their food and reproductive partners, and most of them come to the surface only incidentally. The physical and biotic uniqueness of subterranean ecotope (which is dark, stable, monotonous, hypoxic, hypercapnic, etc.) leads to an adaptive convergence at all levels of organizations (cf., e. g. Nevo and Reig 1990). Consequently these mammals have become unique subjects for studies of (among others) sensory biology and physiology of metabolism.

Particularly Zambian mole-rats of the genus *Cryptomys* (Bathyergidae, Rodentia) have been very intensively studied within the last decade concerning their hearing and acoustic communication (Credner et al. 1996), orientation in space (Burda et al. 1990; Lindenlaub et al. 1995), and physiology af metabolism (Marhold and Nagel 1995; Bennett et al. 1994).

While all these studies have elucidated interesting adaptations to an underground life style, they have been carried out in laboratories, and the central question remains as for how strictly are these animals confined to underground life. Do they also, incidentally or even regularly, come into contact with daylight, aboveground sensory cues or climate? There are only few direct (Genelly 1965; Oatley and Ansell 1966; Sheppe 1973) and indirect observations (e. g. skulls in owl pellets) indicating aboveground activity in mole-rats and related species (cf. De Graaff 1981).

During a six-months' field study in Zambia (April–October 1996) we found some indirect evidence that mole-rats of the genus *Cryptomys* spend more time outside the burrow system than generally assumed. We studied common mole-rats (*Cryptomys* spec., $2n = 68$) in Lusaka and giant mole-rats (*Cryptomys mechowi*) in Ndola. We excavated burrow systems in different areas and caught the animals. Although we never observed mole-rats aboveground, local people and mole-rat hunters reported on mole-rats moving on the surface particularly during early morning hours.

Altogether we excavated 12 nests. Three nests consisted completely of plastic material (nylon stockings, pieces of plastic bags, and sacks). Three further nests contained a mixture of plastic materials, dry grass and root fibres. These six nests were situated near cultivated fields and human buildings. The six remaining nests contained a mixture of grass and root fibres. They were situated far away from human settlements. It seemed that mole-rats preferred plastic materials (if available) to grass or roots. It is obvious that mole-rats must have collected most of their nest material aboveground.

In a food chamber of a colony near Lusaka we found two seeds of the tree *Parinaria curatellifolium* (Chrysobalanaceae). Also this finding indicates that mole-rats may even sometimes forage aboveground.

We found two small colonies of giant mole-rats (3 and 4 animals) in a "dambo" (a seasonally inundated area) near Ndola. Compared to normal habitats (e. g. cultivated fields), the burrow systems from dambos were small (50 m^2 versus >300 m^2). The burrow systems were surrounded by areas where the level of ground water was near or above the surface (at the end of the dry season), so it was impossible for the mole-rats to reach this area underground. Most probably a breeding pair reached the dambo aboveground and established a new colony. This is supported by the finding that both families consisted of two adult animals (male and female) and one or two subadult individuals. Normally, giant mole-rats live in large colonies of even about 40 animals.

These findings indicate that mole-rats of the genus *Cryptomys* obviously spend more time outside their burrows than assumed so far. Most of the aboveground activity occurs probably at night.

Acknowledgement

This work was supported by a travel grant of the DAAD (Deutscher Akademischer Austauschdienst) to A. S.; and was carried out within the framework of the research project "Behavioural ecology and systematics of Zambian mole-rats" (Prof. Dr. H. Burda, Abt. Allgemeine Zoologie, Universität-GH Essen). We thank Prof. Dr. H. Burda for comments on the manuscript and Dr. P. M. S. Phiri (University of Zambia) for the identification of seeds and plants.

References

Bennett, N. C.; Aguilar, G. H.; Jarvis, J. U. M.; Faulkes, C. G. (1994): Thermoregulation in three species of Afrotropical subterranean mole-rats (Rodentia: Bathyergidae) from Zambia and Angola and scaling within the genus *Cryptomys*. Oecologia **97**, 222–227.

Burda, H.; Marhold, S.; Westenberger, T.; Wiltschko, W.; Wiltschko, R. (1990): Magnetic compass orientation in the subterranean rodent *Cryptomys hottentotus* (Bathyergidae, Rodentia). Experientia **46**, 528–530.

Credner, S.; Burda, H.; Ludescher, F. (1996): Acoustic communication underground: Vocalization characteristics in subterranean social mole-rats (*Cryptomys* sp., Bathyergidae). J. Comp. Physiol. A. (in press).

De Graaff, G. (1981): The rodents of Southern Africa. Durban, Pretoria: Butterworth.

Genelly, R. E. (1965): Ecology of the common mole-rat (*Cryptomys hottentotus*) in Rhodesia. J. Mammalogy **46**, 647–665.

Lindenlaub, T.; Burda, H.; Nevo, E. (1995): Convergent evolution of the vestibular organ in the subterranean mole-rats, *Cryptomys* and *Spalax*, as compared with aboveground rat, Rattus. J. Morphol. **224**, 303–311.

Marhold, S.; Nagel, A. (1995): The energetics of the common mole-rat *Cryptomys*, a subterranean eusocial rodent from Zambia. J. Comp. Physiol. B **164**, 636–645.

Nevo, E.; Reig, O. A. (1990): Evolution of subterranean mammals at the organismal and molecular levels. New York: Alan R. Liss.

Oatley, T. B.; Ansell, W. F. H. (1966): *Cryptomys mechowi* above ground. Puku **4**, 193–194.

Sheppe, W. A. (1973): Notes on Zambian rodents and shrews. Puku **7**, 167–190.

Authors' address: Dipl.-Biol. Andreas Scharff, Oliver Grütjen, Abt. Allgemeine Zoologie, FB 9; Universität-GH Essen, D-45117 Essen

Z. Säugetierkunde **62** (1997) 255–256

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Buchbesprechungen

Alt, K. W.; Türp, J. C. (Hrsg.): **Die Evolution der Zähne. Phylogenie – Ontogenie – Variation.** Berlin: Quintessenz-Verlag, 1997. 764 S., 315 Abb., mehrere Tab., Paperback, Preis 198,– DM. ISBN 3-87652-590-X.

Ein Buch zur Odontologie mit hohem Anspruch und bemerkenswertem Umfang ist anzuzeigen. Der Band macht das Bestreben der beiden herausgebenden Zahnmedizner deutlich, ihr Fachgebiet in einen breiten wissenschaftlichen Rahmen zu stellen. In dem Buch, an dem 19 Forscher verschiedener Fachrichtungen als Autoren mitwirkten (drei davon als Verfasser verschiedener „Geleitworte"!), wird der säugetierkundlich interessierte Leser mehrere der Beiträge mit Gewinn lesen.

Nach den erwähnten Geleitworten, einem Vorwort und einem Abschnitt, der die „Wissenschaftlichen Biographien der Autoren" schildert, sowie einer Einleitung der beiden Herausgeber, schließen sich sieben Abschnitte mit insgesamt 24 Kapiteln an, von denen acht sich mit dem menschlichen Gebiß und Kiefergelenk beschäftigen. Die Überschriften der Abschnitte lauten: „Theoretische Grundlagen dar Evolution", „Phylogenese", „Funktions- und Konstruktionsmorphologie", „Odontogenese", „Phylogenese und Ontogenese des Kiefergelenks", „Populationsstudien und Dental-Anthropologie" und „Archäozoologie".

Aus Platzgründen soll hier nicht auf jeden Einzelbeitrag eingegangen werden, doch ist der vergleichende Ansatz vieler Beiträge außerordentlich zu begrüßen. Alt und Türp berichten über vergleichende Odontologie, Wolf schildert die Wechselbeziehungen zwischen Ontogenese und Phylogenese und Bollinger stellt die Entwicklung der Säuger in der Erdgeschichte dar. Morlo bietet einen systematischen Überblick über die Phylogenese der Zähne bei Wirbeltieren, Pfretzscher äußert sich über den Aufbau und die Biomechanik des Zahnschmelzes, sowie über die morphologischen Anpassungen von Säugetierzähnen an die Ernährungsweise. Ferner sei auf das Kapitel von Türp et al. über die stammesgeschichtliche Entwicklung des Kiefergelenks hingewiesen. Auch ein Kapitel von Gutmann über die Entwicklung von der Kiemenreuse zum zahnbesetzten Kieferapparat ist im Zusammenhang mit vergleichenden Darstellungen zu nennen, doch ist nur schwer nachzuvollziehen, daß ein weiterer Beitrag desselben Autors aufgenommen wurde, in dem dieser auf die im vorliegenden Band behandelte Thematik praktisch nicht eingeht, sondern – wieder einmal – versucht, die von ihm stark geprägten Vorstellungen zur Evolution der Organismen als „Das neue Paradigma der Frankfurter Theorie" zu propagieren.

Die Mehrzahl der von den Autoren gebotenen Abbildungen ist anschaulich und instruktiv, nicht nur Strichzeichnungen, sondern auch Halbtonbilder sind in guter Qualität wiedergegeben. Besonders beeindruckten den Referenten die oft mehrseitigen und bis in die neueste Zeit reichenden weiterführenden Literaturverzeichnisse, welche den einzelnen Beiträgen beigegeben sind. Durch sie, wie auch durch die Textdarstellungen, ist der vorliegende Band ein wertvolles Nachschlagewerk für alle, die sich über den Stand der Forschung über die Zähne von Wirbeltieren, insbesondere von Mensch und Säugetieren, informieren wollen. Ein 14 Seiten langes und stark aufgeschlüsseltes Stichwortverzeichnis erhöht die Nutzbarkeit des Werkes.

P. Langer, Gießen

Croft, D. B.; Ganslosser, U. (eds.): **Comparison of Marsupial and Placental Behaviour.** Fürth: Filander Verlag 1996. Paperback, 303 p., numerous illustr. DM 49.80. ISBN 3-930831-02-3.

This stimulating book brings together 13 contributions from different authors, most of them from Australia, but also from Germany, Scotland, and France. It has certainly improved the quality of the book that the two editors submitted the contributions of the authors to competent external reviewers. The articles can be ordered into seven groups, emphasizing different aspects of marsupial behaviour and often comparing it with the behaviour of eutherians.

The sensory system of marsupials is dealt with in a thorough study by Rowe, who gives a well-documented account of sensomotor organisation of the central nervous system. In a second contribution on the sensory system Salamon compiles available data on glands that are olfactorily perceived and on the significance of smelling in social behaviour of 14 marsupial families.

In three contributions different aspects of social behaviour in marsupials are dealt with. Jarman and Kruuk differentiate six "styles" of "spatio-social" organisation, in which they distinguish how adult female marsupials and eutherians defend their range. They were able to differentiate between defence by the single female, by a group of females, or no defence at all. This is combined with the social situations, under which these animals forage, e.g., either solitarily or in ephemeral groups or, thirdly, in persistent groups. The two authors found that most marsupials, in contrast to eutherians, forage solitarily in an undefended range, but there "seem to be no general adaptive reasons for this metatherian failure to evolve sociality or defence of range". In their chapter Jarman and Kruuk mention 14 tables, but only 12 can be found in the text! In two more theoretical contributions both Ganslosser and Hendrichs discuss social interrelationships in marsupials. The latter author emphasizes comparisons between Metatheria and Eutheria.

The subsequent interesting article by Croft discusses interaction of locomotion, foraging competition and group size. The relationship of foraging behaviour with aspects of sociality, such as group size, raises the question how the presence of conspecifics influences the cost of locomotion between food items.

The next set of three articles deals with different behavioural aspects in marsupials, such as reactions towards predators (Coulson), play (Lissowsky) and female mate-choice (Walker).

In reproduction, marsupials are essentially different from eutherians. Ashworth discusses maternal investment in their young and Atramentowicz compares in a stimulating contribution the diversity of ontogenetic periods, such as "strict lactation" and weaning between eutherian Lorisidae and marsupial Delphinidae.

Two articles, one by Winter, the other by Righetti, present comparisons of "pairs" of marsupial and eutherian "ecological equivalents".

The book is concluded by an article from the two editors entitled "Future directions", which gives an unnecessary summary of the above-mentioned articles, but very few perspectives of future research! However, this book as a whole covers a wide range of aspects and offers interesting material. Because of this, the present reviewer regrets the absence of an index, which would have improved the access to the presented data considerably!

P. Langer, Giessen

Instructions to Authors

Submission and Acceptance of Manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel, Germany, e-mail: dkruska@ifh.uni-kiel.de. Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by mail, and as soon as the peer reviews are received the authors will be informed concerning the decision for acceptance.

All correspondence dealing with details of production should be sent to: Zeitschrift für Säugetierkunde, Gustav Fischer Verlag, Villengang 2, D-07745 Jena, Germany.

Form of the Manuscript: Each manuscript should be submitted in triplicate, one original and two copies, in English or German in DIN A4 format either from a typewriter or legible computer print with a left-hand margin of 4 cm and true double spacing.

The first page of the manuscript should contain the following information:
title
name(s) of author(s): full first name for female authors, first initials only for male authors
department and university affiliation
In case of long titles, a running title not exceeding 72 characters should be provided.
Script type should be uniform throughout the manuscript. Use of bold print, italics and spaced-letters must be avoided.
Page footnotes and appendices at the end of the text are not allowed. Names of authors cited in the text are to be underlined in pencil. Botanical and zoological generic and species names should be underlined in pencil with a wavy line, whereby the name of the scientist who first described the species is not underlined.
Authors should indicate in the margins the approximate location in the text for illustrations and tables.
At the end of the manuscript following **References**, the exact postal address(es) of the author(s) should be given.

Content of the Manuscript: Manuscripts can be published as **original investigations** or **short communications.**

a) Original investigations: In addition to the text, original investigations should include illustrations, tables and references, and must not exceed 30 typewritten, double-spaced pages. The text should be divided into: Abstract (in English), Introduction, Material and methods, Results, Discussion (or together as Results and Discussion), Acknowledgements, Zusammenfassung (in German), References.

If written in German, an English title should precede the English abstract; if written in English, a German title should precede a German summary.

b) Short communications: Short communications must not exceed 5 typewritten, double-spaced pages and do not require either an Abstract or Summary. If written in German, an English title should be given on page 1; if written in English, please give a German title on page 1. Short communications need not be headed with subtitles into Introduction, Materials and methods, Results, and Discussion but should be organized according to this form.

Illustrations: Number and size of illustrations must be kept to an absolute minimum. Only well focussed and readily reproducible original prints showing optimal contrast can be accepted; colour plates cannot be processed. Labelling on figures should be uniform, and large and clear enough for eventual reduction in size. On the back of each illustration the following information should be given, using a soft pencil: figure number, name of the journal, first author. Captions to figures should be written on a separate sheet of paper.

Tables: The number and size of tables must be reduced to a minimum. Each table should appear on a separate page including heading and running number.

Comprehensive tables not fitting onto one page should follow on consecutive DIN A4 format sheets of paper.

References: Each paper cited in the text must appear in alphabetical order at the end of the text. Only internationally available literature should be quoted. The names of the journals should be given in abbreviated form in conformity to international use.

Examples
a) From journals:
KALKO, E. K. V; HANDLEY, C. O. JR. (1994): Evolution, biogeography, and description of a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá. Z. Säugetierkunde **59**, 257–273.
b) From books:
HERRE, W.; RÖHRS, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.
c) From reference books:
NIETHAMMER, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. NIETHAMMER und F. KRAPP. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

Printing: The principal author will receive page proofs of the manuscript as well as a set of the illustrations and the original manuscript for proof reading. Only type-setting errors should be corrected. Any major revision undertaken by the author at this stage will result in costs to the authors themselves. The conventional proof-readers' symbols should be used. The corrected page proofs should be signed by the author to indicate that the paper is "ready for print" and be sent to Prof. Dr. Peter Langer, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität Giessen, Aulweg 123, D-35385 Giessen, Germany, e-mail: peter.langer@anatomie.med.uni-giessen.de

Reprints: 50 reprints of each paper are supplied free of charge. When returning the page proofs additional reprints can be ordered at the cost of the author(s).

Publisher: Gustav Fischer Verlag GmbH & Co. KG, Branch Office Jena,. P. O. Box No. 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/6 26-3; Fax ++49(0)36 41/62 65 00; e-mail: office.j@gfischer.de
Advertisement bookings: Enquiries should be directed to Gustav Fischer Verlag, Advertising Manager: Sabine Schröter, P. O. Box 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/62 64 28, Fax ++49(0)36 41/62 64 21
Advertising rates: The price list from February 1, 1997 is effective at present.
Distribution and subscription agency:
For customers **in the German speaking countries:** Please turn to your bookshop or to SFG-Servicecenter Fachverlage GmbH, Zeitschriftenvertrieb: Barbara Dressler, Villengang 2, D-07745 Jena, Germany. Phone ++49(0)36 41/62 64 44, Fax ++49(0)36 41/62 64 43;
For customers **in all other countries:** Please contact your bookshop or Stockton Press., c/o Debbie Floyd, The Subscription Dept., Houndmills, Basingstoke, Hants RG 21 6XS, UK. Phone ++44(0)12 56/35 18 98. Fax ++44/12 56/32 83 39. Subscribers in the **USA** can call toll free on ++1/800/747 3187.
Terms of delivery (1997): 1 volume consisting of 6 issues.
Subscription rate (1997): Price per volume: DM 398.00; ÖS 2 906.00; sFr 382.50; UK Sterling 183.00
Single issue price: DM 80.00; ÖS 584.00; sFr 77.00; UK Sterling 35.00
Reduced membership rates are available on request. Please turn to our publ. house.
All prices mentioned above are exclusive postage. USdollar prices are converted at the current exchange rate. We accept the following credit cards: VISA/Mastercard/American Express, (Please note card-No. and expiry date).
Banking connections:
For customers in the **German speaking countries:**
Deutsche Bank AG Jena, Konto-Nr. 6 284 707, BLZ 820 700 00.
For costumers **in the other countries:**
UK Post Office Giro Account No. 5 192 455. Full details must accompany the payment.
All prices are subject to change without notice.
Subsciption information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting, printing and binding: druckhaus köthen GmbH
Printed in Germany

Abstracted/Indexed in
Animal Breeding Abstracts; Current Contents Agriculture, Biology Environmental Sciences; Biological Abstracts; *BIOSIS* database; Current Advances in Ecological and Environmental Sciences; Dairy Science Abstracts; Fisheries Review; Helminthological Abstracts; Index Veterinarius; South Pacific Periodicals Index; Veterinary Bulletin; Key Word Index to Wildlife Research; Wild Review (Fort Collins); Zoological Record

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

GUSTAV FISCHER

ISSN 0044-3468
Z. Säugetierkunde
Jena · 62(1997)5 · S. 257-320
Oktober 1997

5
1997

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde **62** (1997) 257–264

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Geographical variation in pelage characteristics in *Presbytis comata* (Desmarest, 1822) (Mammalia, Primates, Cercopithecidae)

By V. Nijman

Institute for Systematics and Population Biology, Zoological Museum, University of Amsterdam, Amsterdam, The Netherlands

Receipt of Ms. 19. 07. 1996
Acceptance of Ms. 07. 03. 1997

Abstract

In the traditional view, two subspecies of *Presbytis comata* are present on the island of Java, Indonesia. The nominate form is found in West Java, while on Central Java *P. c. fredericae* is recognised. Geographical variation in *P. comata* has been studied both in museum specimens and in the field. Some alleged differences between the two described forms were found not to be diagnostic, while some intraspecific variation was of a clinal nature, with intermediate populations existing in the eastern part of West Java. It is concluded that a separation of *P. comata* into different subspecies or even species is not warranted.

Introduction

On the island of Java, Indonesia, two single island endemic primate species can be found, both classified as endangered according to I.U.C.N. threat criteria (Eudey 1987): the Javan gibbon *Hylobates moloch* and the Javan grizzled leaf monkey *Presbytis comata* (formerly *P. aygula*, see Weitzel and Groves 1985). The latter species is the subject of this study. Javan grizzled leaf monkey is confined to the rainforests of the western half of the island while some remnant populations are found as far east as Mt. Lawu, on the border of East Java (for a review, see Nijman 1997).

Two subspecies are traditionally recognised: *P. comata comata* (Desmarest, 1822), locally known as Surili, restricted by Sody (1930 b) to West Java, and *P. comata fredericae* (Sody, 1930), locally known as (Lutung) Rekrakan, from Central Java. Eudey (1987) states that *P. c. fredericae* is known with certainty only from Mt. Slamet, although Bartels (1937) reported the occurrence of the species on Mts Dieng and some specimens have been collected on Mts Dieng and Mt. Lawu. During the last few years it has become apparent that *P. comata* still prevails in those areas in Central Java from which it was historically known (Seitre and Seitre 1990; Nijman and Sözer 1995; Nijman 1997). Recently *P. c. fredericae* has been proposed as a separate species *P. fredericae* by I. U. C. N. (1994) and Brandon-Jones (1995, 1996). The pelage colour of adults is the most striking difference between the two types: *fredericae* differs from the nominate race in having black upper parts instead of grey, and the under parts are black apart from the lower abdomen, innerside of the legs, which are white, and the upper part of the chest, which is whitish or light grey. Hence, the proposed English names of Javan grizzled leaf monkey for *P. comata* and Javan fuscous leaf monkey for *P. fredericae* (I. U. C. N. 1994). If *P. c. fredericae* is considered to be a separate species it undoubtedly can be ranked among the rarest and most endangered primate species in the world, making it a top priority for

primate conservation (cf. Brandon-Jones 1995). It would be restricted to four isolated forest areas viz. Mt. Slamet, Mt. Cupu-Simembut, Mts. Dieng and Mt. Lawu (Nijman 1997), in a province with one of the highest human population densities of Indonesia. None of the forests are adequately protected and two of them, the first and the latter of the localities mentioned above, are situated on an active volcano.

The aim of this study is to describe the geographical variation in pelage characteristics that can be observed among populations of *P. comata*. Data collected in the central parts of Java, combined with data obtained from the study of museum specimens, form the basis of these descriptions.

Material and methods

A total of 52 museum specimens in the National Museum of Natural History, Leiden (RMNH), the Zoological Museum, Bogor (MZB), and the British Museum of Natural History (BMNH), London were examined, viz. 29 from the western province and 10 from the central Javan province. For another 13 specimens studied, no locality was given.

During surveys over a 10-month period in 1994 and 1995 in the central part of Java, i.e. the eastern part of West Java, Central Java, and the western part of East Java, descriptions of external appearance and pattern of coloration of *P. comata* were made. Populations in the western half of West Java were studied in order to obtain data on the external appearances of the species in this area. The number of animals and number of neonates of which a clear view was obtained per mountain complex was estimated by summation of the maximum number of individuals observed at different localities throughout the mountain complex. When a group was observed at a locality where it had been seen previously or when there was doubt whether a particular animal was previously encountered or was in fact a different individual, a description was made, but it was not included in the total estimate of numbers. No specimens were collected and the descriptions are exclusively based on field observations and museum specimens.

Results

P. comata was observed in 6 forest areas. The areas in which the species was observed included (estimated numbers of clearly observed individuals plus neonates are given in parenthesis): Mt. Pancar (5), Mt. Gede-Pangrango (20 + 3), Mt. Sawal (3 + 1), Mt. Slamet (16 + 3), Mts. Dieng (29 + 3), Mt. Lawu (0).

Typical *P. comata comata* from the western part of West Java (e.g. Mt. Pancar [106°54′ E, 6°35′ S], Mt. Gede-Pangrango [107°00′ E, 6°45′ S]) has a rather dark grey dorsum with the hair on the back being longer than on the tail, legs and arms. The tail is dark grey to blackish, and arms and legs are dark grey, often darker than the back. The venter, innerside of arms and legs, and innerside of the tail are whitish. The species has a blackish prominent crest. In some individuals the hair on the back is rather short while in others it is longer. In individuals with longer hair the upper-coat is formed by longer dark grey or blackish hair while the under-coat consists of short dark grey hair.

In some individuals the white venter is intermingled with some grey hairs originating from the flanks, and the impression arises that the venter of animals from the western part of West Java (e.g. Mt. Salak [106°45′ E, 6°45′ S]: RMNH 34335, 34336, 34338, 51891) is less intermingled with grey than in specimens originating from areas somewhat further to the east e.g. in the mountains south of Bandung (e.g. Mt. Tilu [107°30′ E, 7°09′ S]: RMNH 26820). However, as no field observations were made in the latter area, the question to what extent the venter shows greyish parts in these areas must remain unanswered.

P. comata from Mt. Sawal [108°16′ E, 7°12′ S] in the eastern part of West Java, is somewhat different in colouration from those in areas to the west and to the east. The dorsum

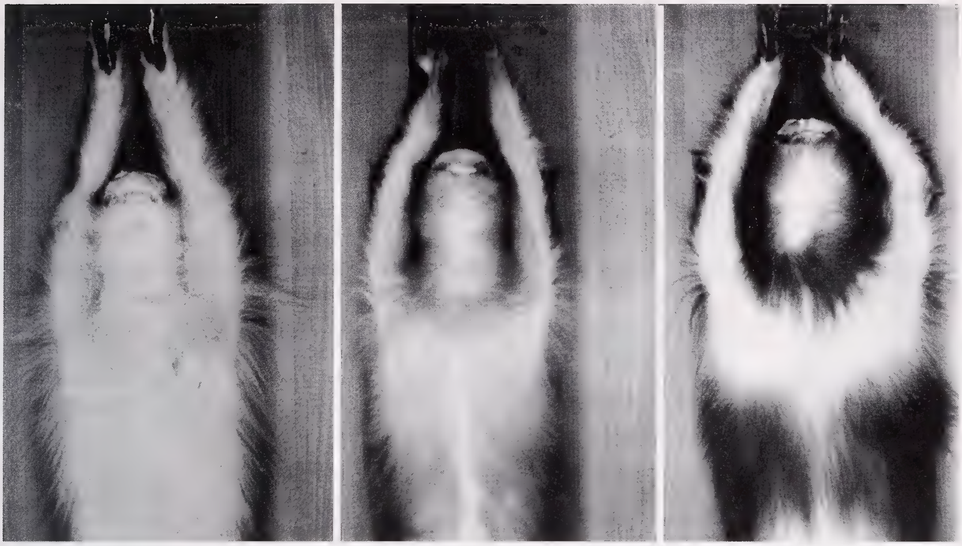


Fig. 1. Geographical variation in pelage characteristics of the venter in *Presbytis comata*. From left to right: RMNH 26 824, Tapos, Mt. Salak, West Java; RMNH 34 296, Ceringin, West Java near border with Central Java; RMNH 34 346, Tegal Sari, Mt. Slamet, Central Java.

is not different from animals to the west, although in the animals studied it is rather dark. The arms are very dark grey, almost black. The venter consists of a whitish or light grey throat, edged on the upper side of the breast by a broad grey band. This band originates from the flanks and is narrower in the centre, with a thin whitish cross band. The lower abdomen, innerside of arm, legs and tail are whitish. The same pattern of coloration, but less pronounced, was found in a skin labelled *P. aygula aygula* and collected at Ceringin/ Cisaga [108°30′ E, 7°27′ S] near Banjar, West Java, near the border with Central Java (RMNH 34 296) (Fig. 1). This individual has rather dark arms, although at Mt. Sawal the animals had even darker arms.

In typical *P. comata fredericae* from Mt. Slamet [109°13′ E, 7°19′ S] or Mt. Prahu [109°55′ E, 7°20′ S] (e. g. MZB 2 993, 2 994, 2 995, RMNH 14 612) the dorsum is black, the throat and upper chest are white or light grey, the lower abdomen, innerside of the legs, arms and tail are white, while the remainder is black with a thin nearly white cross band. At the lower elevations of Mts. Dieng, near the village of Linggo, the same black form is present, but most of the animals are less dark in colour. The pattern of coloration is the same as in the typical form, but the dorsum is more greyish, not black, and resembles those of the Mt. Sawal animals. For an overview of pelage characteristics based on field observations, see table 1.

P. comata has been observed in both primary and secondary forest, in ecotones and in the forest interior. The species is present in lowland forests, in forests on steep slopes and hills, and in montane and upper montane forests. There is no differentiation in habitat or altitudinal preferences between populations in the east or west. In behavioural terms all forms are indistinguishable from one another. Most notably the vocalisations, in particular the alarm call, of animals on Mt. Gede-Pangrango, Mt. Sawal, Mt. Slamet, Mts. Dieng and Mt. Lawu are qualitatively similar (cf. Bartels 1937). In other *Presbytis* species, e. g. those on Sumatra, the different species are readily distinguished by their specific vocalisations (see e. g. Wilson and Wilson 1977; Aimi and Bakar 1992, 1996).

Sody (1930 b) noted that inhabitants of the Mt. Slamet region, where he obtained the specimens described as *fredericae*, were not familiar with the Javan native name Surili,

Table 1. Pelage characteristics of *Presbytis comata* based on field observations on 5 mountain complexes on Java, listed from west to east. The number of individuals of which a clear view was obtained is given in parenthesis.

locality	venter	dorsum	arms	dorsum neonate
Mt. Pancar	white (4)	(dark) grey (5)	dark grey (5)	–
Mt. Gede-Pangrango	white (20)	(dark) grey (20)	(dark) grey (20)	grey (3)
Mt. Sawal	white with dark grey band on breast, narrow in centre (3)	dark grey (3)	blackish (3)	dark grey (1)
Mt. Slamet	white with black band on breast (16)	black (16)	black (16)	black (3)
Mts Dieng	white with dark grey band on breast (22)	dark grey (22)	dark grey (22)	dark grey (3)
	white with black band on breast (2)	black (7)	black (7)	–

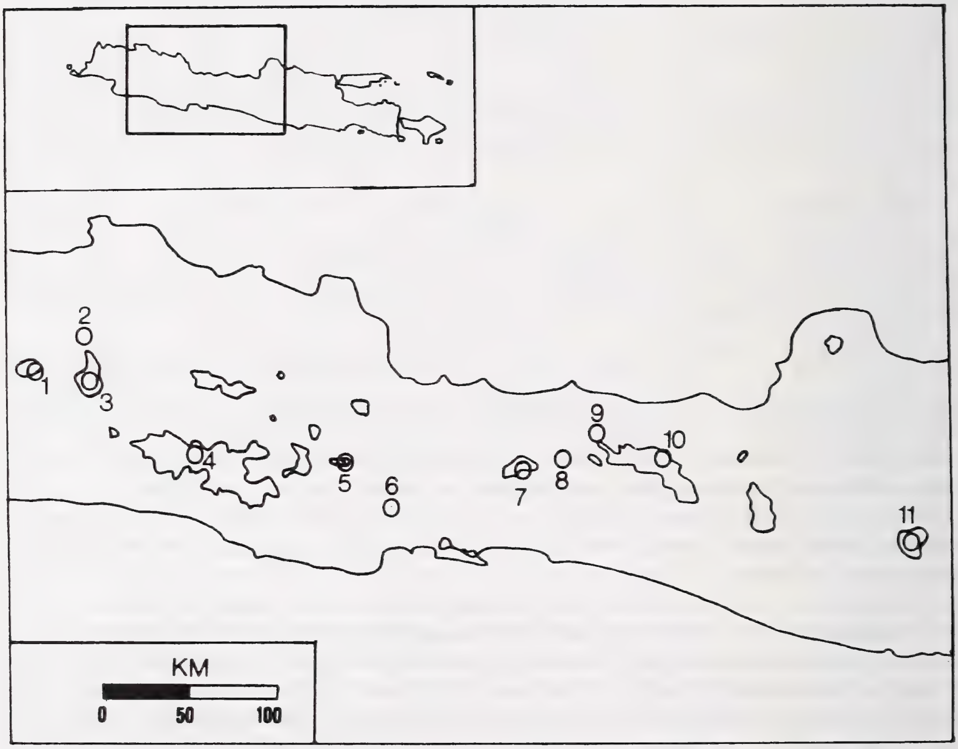


Fig. 2. Map of the central part of Java, Indonesia, with the localities mentioned in the text. Key: 1. Mt. Salak; 2. Mt. Pancar; 3. Mts Gede-Pangrango; 4. Mt. Tilu; 5. Mt. Sawal; 6. Ceringin/Cicaga; 7. Mt. Slamet; 8. Mt. Cupu-Simembut; 9. Linggo; 10. Mt. Prahu (the area between Linggo and Mt. Prahu is known as Mts Dieng); 11. Mt. Lawu. The drawn lines on the map indicate the 1 000 m contour lines.

nor did they made a linguistic distinction between *P. comata* and the sympatric Ebony leaf monkey *Trachypithecus auratus*; both species were named Lutung (Sody 1930 a). In West and Central Java, and Bali, Lutung is the name used for the more common and more widespread Ebony leaf monkey, while in East Java it is named Budeng. Bartels (1937) reported that *P. comata* was known as Rekrekan in the Mts. Dieng region. Interviews with people living near the forest areas by the present author revealed that *P. comata* is locally known as Surili east to Mt. Sawal, and from Mt. Slamet to Mts. Dieng it is known as (Lutung) Rekrakan/Rekrekan. In some areas, e. g. on Mt. Prahu and Mt. Lawu, some informants were aware of the presence of two types of leaf monkeys, but both of them were called Lutung (Mt. Prahu and Mt. Lawu) or Budeng (Mt. Lawu). The linguistic separation between *fredericae* and *comata* in Rekrakan and Surili respectively, is accounted for by the two different languages, Javanese and Sundanese, spoken in different parts of the island and is not of biological significance. The name Rekrakan, however, is also used for the red form of the Ebony leaf monkey in the Malang region, East Java (Rudiyanto, pers. comm.).

Discussion

Intraspecific variation, in particular the coloration and pattern on the venter, in *Presbytis comata* is not geographically disjunct but seems to be of a clinal nature with intermediate populations existing in areas between those from where the two subspecies have been described. Whether or not more populations of the species remain in these intermediate areas remains unclear. Since today large areas of Java have been deforested, populations of *P. comata* are found scattered throughout West and Central Java. However, there seems to be no major gap in the species distribution between West Java and Central Java, nor does there seem to be a geographical or ecological barrier in the intermediate area that can explain a possible separation between populations east or west of the provincial boundary.

One of the morphological characters on which the separation between *comata* and *fredericae* has been based, namely the dorsal coloration, shows, at least in the populations on the Dieng mountains, considerable variation and cannot be used as a diagnostic character.

On the basis of the data presented above, it can be concluded that the separation of western and eastern populations of *P. comata* into two different species is not warranted. Neither form can be recognised as a diagnosably distinct taxon and therefore the appropriate name for the species remains *P. comata*. For those who do not wish to abandon the use of trinomials, it should be understood that these can only be used to identify populations within a continuum of geographical variation. The geographical limits of these populations will, however, remain arbitrary.

The tripartite distribution of the grey leaf monkeys of the genus *Presbytis* in the Sundaic region, currently known as *comata* (western Java), *thomasi* (northern Sumatra), and *hosei* (northeastern Borneo), has been a long-time issue of debate. Pocock (1934) considered these taxa as constituting four different species, including two on Borneo (*sabana* and *hosei*: in Borneo some populations show adult sexual dimorphism in crest shape and extent of white on the brow while others are monomorphic, resulting in the description of a number of (sub)species). Chasen (1940) subsequently considered them to be races of a single species, *P. comata*, as did some authors afterwards, e. g. Hooijer (1962). This made *P. comata* a polytypic species, with a distribution following the periphery of Sundaland. The three zones were regarded as areas of convergent evolution by Medway (1970) and in his more cautious interpretation the three forms (*comata*, *thomasi*, and *hosei*) were considered to be separate species, a view supported by Groves (1970) and most subsequent workers (Napier 1985;

Weitzel et al. 1988; Corbet and Hill 1992; I. U. C. N. 1994). In contrast, Brandon-Jones (1978, 1984, 1993, 1996), regarded them as relicts of a single population, differentiated at the subspecific level, in which the grey-backed taxon is perceived as a relict in its present disjunctive distribution, representing an earlier coloniser of the Sundaic region. Brandon-Jones (1993) postulated that the phylogeny of the genus involves unidirectional integumental colour degradation, comparable with Hershkovitz' (1968) theory of metachromism. In this view the pelage colour of the preglacial relict species in the genus *Presbytis* is predominantly black (Brandon-Jones 1978, 1993), after which bleaching occurs via the eumelanin pathway from (brown to) grey to white (Hershkovitz 1968). Thus, those mammalian species that are characterised by a very dark/black coloration can, generally, be regarded as progenitors of all living members of their group. If we follow the Brandon-Jones (1987, 1993) model and accept the predominant glossy black *P. potenziani*, from the Mentawai islands of the west coast of Sumatra, as the sole representative of the genus during a Pleistocene period of climatic deterioration, after which it evolved (or "degenerated" as preferred by Brandon-Jones 1993) into the grey *P. comata* (sensu lato) then the present occurrence of melanistic individuals in that taxon needs further explanation.

The present finding of populations intermediate in coat coloration and pattern and the presence of greyish individuals in the easternmost populations of *P. comata*, show that the species is more variable in its pelage coloration than previously assumed. If *P. comata* from Java is considered conspecific with *P. thomasi* and *P. hosei*, intraspecific variation in pattern and coloration below the head (which is generally more conservative than the pelage colour itself: Wilson 1978; Wilson and Wilson 1977) in the Javan populations would be larger than variation between *comata*, and extralimital *thomasi* and *hosei*.

In conclusion, *P. comata* on Java cannot be separated into two different subspecies or even species as neither form can be recognised as a diagnosably distinct taxon. Moreover, the large variation in pelage characteristics within the Javan populations makes it increasingly more difficult to consider them conspecific with the other grey-backed leaf monkeys – *P. thomasi* and *P. hosei* – from north Sumatra and northeastern Borneo, respectively.

Acknowledgements

I wish to thank Mr Boeadi of the Zoological Museum Bogor, Dr C. Smeenk of the National Museum of Natural History, Leiden, and Miss P. Jenkins of the British Museum for Natural History, London for allowing me to examine specimens in the collections under their care, Dr P. J. H. van Bree, Sara Booth, Dr C. J. Hazevoet and an anonymous reviewer for constructive comments on the manuscript, and Stephan Könemann for the German translation of the abstract. Research on Java was made possible due to the co-operation of the Indonesian Institute for Science (LIPI) and the Directorate General of Forest Protection and Nature Conservation (PHPA). Finally, Dr P. J. H. van Bree is thanked for his help and support throughout the study.

Zusammenfassung

Geographische Variation von Fellbesonderheiten bei Presbytis comata (Desmarest, 1822) (Mammalia: Primates: Cercopithecidae)

Aus traditioneller Sicht sind zwei Unterarten von *Presbytis comata* auf der Insel Java beschrieben. Während *P. c. comata* in West-Java gefunden wird, gilt *P. c. fredericae* als anerkannte Unterart Zentral-Javas. Die geographische Variation von *P. comata* wurde sowohl im Feld als auch anhand von Museumsmaterial studiert. Es stellte sich heraus, daß manche Unterschiede der beiden beschriebenen

Formen nicht diagnostisch verwertbar waren, während einige intraspezifische Variationen, bei Berücksichtigung von intermediären Populationen, einen klinalen Charakter besaßen. Es kann die Schlußfolgerung gezogen werden, daß die Trennung der zwei Formen in verschiedene Unterarten oder Arten nicht gerechtfertigt ist.

References

AIMI, M.; BAKAR, A. (1992): Taxonomy and distribution of *Presbytis melalophos* group in Sumatera, Indonesia. Primates **33**, 191–206.

AIMI, M.; BAKAR, A. (1996): Distribution and deployment of *Presbytis melalophos* group in Sumatera, Indonesia. Primates **37**, 399–409.

BARTELS, M. (1937): Zur Kenntnis der Verbreitung und der Lebensweise javanischer Säugetiere. Treubia **16**, 149–164.

BRANDON-JONES, D. (1978): The evolution of recent Asian Colobinae. In: Recent advances in primatology, Vol 3: Primate evolution, Proceedings of the sixth congress of the International Primatological Society, 1976. Ed. by D. J. CHIVERS and K. A. JOYSEY. London: Academic Press. Pp. 323–325.

BRANDON-JONES, D. (1984): Colobus and leaf monkeys. In: The encyclopaedia of mammals. Vol. 1. Ed. by D. MACDONALD. London: Allen and Unwin Pp. 398–408.

BRANDON-JONES, D. (1993): The taxonomic affinities of the Mentawai Islands Surili, *Presbytis potenziani* (Bonaparte, 1856) (Mammalia: Primates: Cercopithecidae). Raff. Bull. Zool. **41**, 331–357.

BRANDON-JONES, D. (1995): *Presbytis fredericae* (Sody, 1930), an endangered colobine species endemic to Central Java, Indonesia. Primate Conserv. **16**, 68–70.

BRANDON-JONES, D. (1996): The Asian Colobinae (Mammalia; Cercopithecidae) as indicators of Quaternary climatic change. Biol. J. Linn. Soc. **59**, 327–350.

CHASEN, F. N. (1940): A handlist of Malaysian mammals. Bull. Raffles Mus. **15**, 1–209.

CORBET, G. B.; HILL, J. E. (1992): The mammals of the Indomalayan region: a systematic review. Oxford: Nat. Hist. Mus. Publ. Oxford Univ. Press.

EUDEY, A. A. (1987): Action plan for asian primate conservation: 1987–1991. Gland: IUCN/SSC Primate Specialist Group.

GROVES, C. P. (1970): The forgotten leaf-eaters, and the phylogeny of the Colobinae. In: Old World monkeys: evolution, systematics and behavior. Ed. by J. R. NAPIER and P. H. NAPIER. New York: Academic Press. Pp. 555–587.

HERSHKOVITZ, P. (1968): Metachromism or the principle of evolutionary change in mammalian tegumentary colors. Evolution **22**, 556–575.

HOOIJER, D. A. (1962): Quaternary langurs and macaques from the Malay Archipelago. Zool. Verh. Leiden **55**, 1–64.

I. U. C. N. (1994): Preliminary list of Asian primate taxa (November 1994). Gland: I.U.C.N./S.S.C. Primate Specialist Group.

MEDWAY, LORD (1970): The monkeys of Sundaland: ecology and systematics of the cercopithecids of a humid equatorial environment. In: Old World monkeys: evolution, systematics and behavior. Ed. by J. R. NAPIER and P. H. NAPIER. New York: Academic Press. Pp. 513–553.

NAPIER, P. H. (1985): Catalogue of primates in the British Museum (Natural History) and elsewere in the British Isles. Part III: Familie Cercopithecidae, subfamily Colobinae. London: British Museum (Natural History).

NIJMAN, V. (1997): On the occurrence and distribution of *Presbytis comata* (Desmarest, 1822) (Mammalia: Primates: Cercopithecidae) in Java, Indonesia. Contr. Zool., Amsterdam (in press).

NIJMAN, V.; SÖZER, R. (1995): Recent observations of the Grizzled leaf monkey (*Presbytis comata*) and an extension of the range of the Javan gibbon (*Hylobates moloch*) in Central Jawa. Trop. Biodiv. **3**, 45–48.

POCOCK, R. I. (1935): The monkeys of the genera *Pithecus* (or *Presbytis*) and *Pygathrix* found to the east of the Bay of Bengal. Proc. Zool. Soc. Lond. **1934**, 895–961.

SEITRE, R.; SEITRE, J. (1990): Recent sightings of rare primates on Java. Primate Conserv. **11**, 18.

SODY, H. J. V. (1930 a): *Pithecus aygula fredericae* n. subsp. Trop. Natuur **19**, 68.

SODY, H. J. V. (1930 b): On some new and insufficiently known mammals from Java, Borneo and Celebes. Natuurkd. Tijdschr. voor Ned. Indië **90**, 258–273.

Wilson, W. L. (1978): Variation among primate populations in Sumatra. In: Recent advances in primatology. Vol 3: Primate evolution, Proceedings of the sixth congress of the International Primatological Society, 1976. Ed. by D. J. Chivers and K. A. Joysey. London: Academic Press. Pp. 311–313.

Wilson, C. C.; Wilson, W. L. (1977): Behavioral and morphological variation among primate populations in Sumatra. Yb. Phys. Antropol. **20**, 207–233.

Weitzel, V.; Groves, C. P. (1985): The nomenclature and taxonomy of the colobine monkeys of Java. Int. J. Primat. **6**, 399–409.

Weitzel, V.; Yang, C. M.; Groves, C. P. (1988): A catalogue of primates in the Singapore Zoological Reference Collection, Department of Zoology, National University of Singapore (formerly the Zoological Collection of the Raffles Museum). Raffles Bull. Zool. **36**, 1–166.

Author's address: Vincent Nijman, Institute for Systematics and Population Biology, Zoological Museum, University of Amsterdam, P.O. Box 94 766, 1090 GT Amsterdam, The Netherlands.

Z. Säugetierkunde **62** (1997) 265–280

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Morphological versus chromosomal and molecular divergence in two species of *Eligmodontia*

By R. S. Sikes, J. A. Monjeau, E. C. Birney, C. J. Phillips, and Jeanna R. Hillyard

Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota, USA, Departamento de Ecología, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina, and Department of Biology, Illinois State University, Normal, Illinois, USA.

Receipt of Ms. 14. 11. 1996
Acceptance of Ms. 17. 03. 1997

Abstract

Karyotypic and mtDNA variation support the presence of at least two distinct species of *Eligmodontia* in the Patagonian region of Argentina. No diagnostic morphological characters are available to identify these species reliably, and few data are available to assess reliably the degree of morphological difference between them. We used univariate and multivariate analyses of external morphological and cranial characters in a sample of *Eligmodontia* collected at 15 localities across northern Patagonia to test the hypothesis that these presumed species (*Eligmodontia typus* and *E. morgani*) also are morphologically distinct. No single diagnostic morphological character was identified based on specimens for which independent identifications were available through mtDNA sequence and species-specific diploid numbers. However, discriminant function analyses were able to assign specimens reliably to correct species as independently determined. Cluster analyses based on various combinations of morphological characters showed some congruence with the other data sets, but specimens of known mtDNA haplotype did not cluster together exclusively. These patterns suggest that although the genetic and karyological differences are substantial and potentially represent a deep divergence, these changes are not mirrored by equivalent morphological divergence.

Introduction

Silky mice of the phyllotine genus *Eligmodontia* occupy arid habitats over a large geographic portion of South America from southern Perú to the southern Patagonian region of Argentina. Hershkovitz (1962) noted that as many as 20 species-group names were commonly used for members of this genus prior to his revision in which he recognized only a single species, *E. typus*, with two subspecies. Hershkovitz's (1962) work was based on morphology, and thus by lumping all previously recognized taxa as a single species he acknowledged the relatively low degree of morphological divergence within the genus. Despite more than 30 years of research on this genus and the fact that several species presently are recognized (Musser and Carleton 1993), there still are no diagnostic morphological characters available to assign specimens of *Eligmodontia* reliably to species. Lack of diagnostic characters hinders all aspects of biological research, as even such fundamental tasks as alpha-level faunal surveys and delineation of species distributions require unequivocal specimen identification. We now have a sample of *Eligmodontia* from northern Patagonia representing two species, *E. typus* and *E. mor-*

gani, for which unequivocal identification based on karyotypic and mtDNA data are available (see Hillyard et al. 1997). This unique sample makes it possible for us to: 1) assess the degree of morphological divergence between the two species; 2) assess how well previously described morphological characters distinguish between them; and 3) search for diagnostic morphological characters or character combinations that allow reliable species identification.

Cytogenetic studies by Ortells et al. (1989), Kelt et al. (1991), Zambelli et al. (1992), and Spotorno et al. (1994) have reported diploid chromosomal numbers of 50, 43–44, 32–33, and 34 for specimens of *Eligmodontia*, and the names *E. puerulus*, *E. typus*, *E. morgani*, and *E. moreni*, respectively, were associated with these cytotypes by Kelt et al. (1991) and Spotorno et al. (1994). Further evidence of species-level or deeper differences within *Eligmodontia* is provided by Hillyard et al. (1997). They sequenced a 348 base-pair region of the cytochrome b gene of specimens of *Eligmodontia* and found two haplotypes that corresponded exactly to the karyotypically distinct *E. typus* and *E. morgani* and differed from each other by as much as 11.8%. In a recent morphological study Braun (1993) recognized six species of *Eligmodontia* in her treatment of phyllotine rodents and showed discrete separation of each species in distance dendrograms. However, clustering methods such as those used by Braun (1993) will find differences between operational taxonomic units (OTU's) regardless of whether or not there are biologically meaningful differences (Engstrom et al. 1994), and the basis for her a priori recognition of six species was not presented.

Given that phyllotine rodents have been present in southern South America for at least several million years (Patterson and Pascual 1972; Marshall 1979; Reig 1978) and that *Eligmodontia* are geographically widespread, karyotypic and chromosomal divergence within the genus is not surprising. However, these molecular and chromosomal differences seem not to be matched by comparable morphological divergence. The apparent high degree of similarity among some species of *Eligmodontia* could arise through (1) wide-spread introgressive hybridization, (2) relatively recent genetic isolation events that have not allowed sufficient time for species to undergo morphological divergence comparable to that observed in molecular and chromosomal data, or (3) selection favoring a similar phenotype among species that is greater than any selection favoring phenotypic divergence.

Materials and methods

We collected specimens used in these analyses on two expeditions (1992 and 1995) to various localities in the Argentine portion of Patagonia. Voucher specimens presently are deposited in the University of Minnesota Bell Museum of Natural History, St. Paul, MN, and the tissue specimens at Illinois State University, Normal, IL. Tissues used for molecular analyses were removed from fresh animals and immediately frozen in liquid nitrogen (for further details see Hillyard et al. 1997). In 1995 we also prepared chromosome spreads following the technique described by Patton (1967) and modified by Lee and Elder (1980) for a subset of animals captured. These karyotypic data were used to assign mtDNA genotypes to species as defined by Kelt et al. (1991) and Ortells et al. (1989). We measured 18 cranial characters (Fig. 1) to the nearest 0.01 mm with digital calipers from all of our adult specimens (including those with and without independent identifications) and recorded four external body measurements (total length, tail length, hind foot length, and ear length) and sex from specimen labels. We also calculated measurements for 5 characters used by Braun (1993).

Only animals with completely erupted dentition were considered to be adult. These adult specimens were placed into three age groups based on tooth wear following criteria specified by Pearson et al. (1987). Categories used were: N if no wear was evident on M^2, W if wear was evident on M^2 but cusps were still distinct, and O if cusps were no longer distinct on M^2. We ordered individuals based on scores for the discriminant multipliers obtained from the canonical discriminant function analysis and assessed the placement of individuals in this list based on their age category assignment. No pattern of age varia-

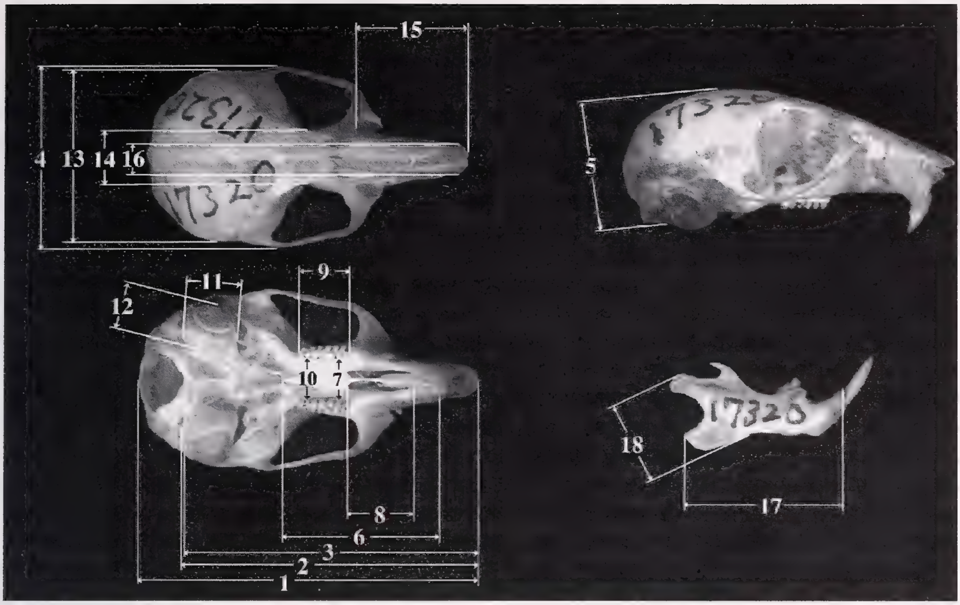


Fig. 1. Digitized image of a skull of *Eligmodontia morgani* illustrating the cranial measurements included in morphological analyses. Numbers represent the following measurements: 1) greatest length of skull; 2) condylobasal length; 3) basal length; 4) zygomatic breadth; 5) greatest depth of skull; 6) length of palate; 7) palatal width at M^1; 8) length of incisive foramen; 9) length of maxillary toothrow; 10) palatal width at M^3; 11) length of auditory bullae; 12) breadth of auditory bullae; 13) breadth of braincase; 14) least interorbital breadth; 15) rostral length; 16) nasal breadth; 17) mandibular length; 18) mandibular height.

tion was revealed, so all individuals classified as adult were included in subsequent analyses and age variation is not discussed beyond. Our data set of adults included 53 animals for which independent identification was available and 124 specimens that lacked independent verification of species assignment. Sample sizes differ slightly among statistical comparisons that follow because only specimens with no missing data for any character were included in multivariate analyses.

Because species identifications in mammals typically are made using cranial or external measurements rather than karyotypes or DNA sequences, our first priority was to perform univariate analyses on morphological characters to try to identify diagnostic characters and to assess variation in individual characters. We used one-way analysis of variance (ANOVA) to test for differences in mean size of each character examined between species and between sexes (excluding the ratios used by Braun 1993). We used Type III Sums of Squares (SS) errors in the General Linear Models (GLM) package of SAS to determine statistical significance (SAS Institute Inc. 1990). Because many one-way comparisons were to be made with each data set, we used a sequential Bonferroni α adjustment to maintain an experimentwise error rate $\leq 5\%$ (Rice 1989). In these analyses we made 18 one-way comparisons on our morphological characters (including cranial and standard external characters).

We next performed separate cluster analyses on standardized data using all of the cranial and external body measurements with the NT-SYS package (Rohlf et al. 1982) without regard to independent identification based on mtDNA sequences or karyotypes. These cluster analyses were performed to see if specimens could be separated accurately when multiple characters were considered simultaneously. We then performed a similar cluster analysis using only those characters that Braun (1993) found useful in distinguishing between these two species. These characters were: 1) relative tail length (mean tail length divided by mean head-body length); 2) relative ear length (mean ear length divided by mean head-body length); 3) relative hind foot length (mean hind foot length divided by mean head-body length); 4) inflation of tympanic bullae (mean bullar length times mean bullar width divided by mean greatest skull

length); and 5) relative toothrow length (mean maxillary toothrow length divided by mean greatest skull length). Because one cannot make a priori species identifications to obtain means for the ratios used by BRAUN (1993), we calculated the ratios using measurements obtained for each individual. We next tested for normality in each of the cranial characters using the Wilks-Shapiro statistic with $\alpha = 0.05$ for significance. These results indicated that four cranial characters: 1) palatal width at M^1; 2) palatal width at M^3; 3) rostral length; and 4) breadth of braincase were not normally distributed and these characters were excluded from further analyses. External body measurements were not tested for normality because some (e. g., hind foot length and ear length) were integer values over only a small range.

We next were interested in determining how well the specimens of known species affiliation could be separated in multivariate character space using each of the data sets considered above. We used discriminant function analysis to assess the utility of morphological data sets (cranial, standard external, and those characters used by BRAUN 1993) for distinguishing between these two species. Following these discriminant function analyses we used step-wise discriminant function analysis on each data set to identify those characters best able to distinguish between them. Because discriminant function analyses resulted in species separation only in multidimensional space, we next used canonical discriminant function analysis to reduce the dimensionality to the first two canonical dimensions and to compute the raw canonical coefficients that resulted in maximum separation on each axis.

To assess the power of our discriminant function obtained from the previous analyses to assign unidentified specimens to species, we used our sample of animals of known identity as a training set to classify the 124 specimens for which neither mtDNA nor karyotypic data were available. Probability of group membership was calculated based on discriminant scores. We examined a plot of all specimens based on values computed from canonical coefficients that were derived from specimens of known identity (see above) to gain some insight as to the degree to which the specimens clustered into discrete groups.

Because each of the data sets did provide some independent discriminatory power, we next considered all variables in a similar analysis. We again used a stepwise discriminant function to identify the subset of characters best able to classify specimens of known identity correctly. We then performed a discriminant function analysis considering only these characters to classify unknown specimens and computed probability of group membership. We used canonical discriminant function analysis to compute canonical coefficients for the first two eigenvectors derived from those discriminatory variables. Using these canonical coefficients, we computed scores for all specimens and plotted individuals in this two-dimensional space. All analyses except for the cluster programs were performed in SAS (SAS Institute Inc. 1990).

Results

Our karyotypic analyses of a subset of animals (n = 15) collected in 1995 support the conclusions of ORTELLS et al. (1989), KELT et al. (1991), and ZAMBELLI et al. (1992) in that we found diploid numbers of 43–44, and 32–33 and clear morphological differences (number and size of metacentrics) for *Eligmodontia typus* and *E. morgani*, respectively. Furthermore, these karyotypes were matched unequivocally to mtDNA haplotypes from tissues taken from the same specimens (HILLYARD et al. 1997). By establishing a definite correspondence between mtDNA haplotypes and karyotypes with a subset of individuals, we then were able to assign individuals of known mtDNA haplotypes reliably to species even though corresponding karyotypes were not available. This greatly augmented sample sizes available for morphological comparisons.

Univariate analyses produced no significant differences between the sexes for any character in either species. We detected significant differences between the two species in only 7 of the 18 characters examined using the conservative rejection criterion of the sequential Bonferroni adjustment (Tab. 1). A comparison of means showed that specimens of *E. typus* tended to be larger than those of *E. morgani* for five of these characters, whereas *E. morgani* was larger than *E. typus* for two others. The percent difference between the species for these characters ($\bar{x}$ for *E. typus*/$\bar{x}$ for *E. morgani*) ranged from 19% larger for tail length and 13% larger for ear length in *E. typus* as compared to *E. morgani* and 6% smaller for length of the incisive foramina and 7% smaller for nasal width in

Table 1. Means, ranges, relative differences (*typus*/*morgani*), and overlap in the 10 morphological characters that showed the greatest differences between *Eligmodontia typus* and *E. morgani* in univariate analyses. Differences in character means marked with an asterisk were statistically significant with α levels determined by a sequential Bonferroni adjustment to maintain an error rate of 5% across analyses.

Character	n (t, m)	*E. typus*		*E. morgani*		Relative difference	Overlap	P value
		$\bar{x}$	Range	$\bar{x}$	Range			
total length	31,22	175.84	151–205	166.36	146–197	1.06	151–197	0.0112
tail length	31,22	92.71	77–104	78.05	69–90	1.19	77–90	0.0001*
hind foot	31,22	23.13	22–25	22.27	21–25	1.04	22–25	0.0050
ear	31,22	18.05	16–22	16.00	14–19	1.13	16–19	0.0001*
incisive foramen	31,22	4.91	4.34–5.61	5.25	4.72–6.04	0.94	4.72–5.61	0.0007*
maxillary toothrow	31,22	3.74	3.45–3.97	3.60	3.33–3.88	1.04	3.45–3.88	0.0004*
bullar length	31,22	4.05	3.80–4.34	3.61	3.10–4.09	1.12	3.80–4.09	0.0001*
bullar breadth	31,22	4.31	3.91–4.77	4.12	3.75–4.40	1.05	3.91–4.40	0.0003*
nasal breadth	31,21	2.36	2.04–2.61	2.54	2.20–2.88	0.93	2.20–2.61	0.0001*
mandibular height	31,20	5.77	5.22–6.53	5.54	4.92–6.44	1.04	5.22–6.44	0.0304

E. typus. The fact that only 7 characters showed significant differences and that the differences tended to be small illustrate that relatively little morphological difference exists between these species in univariate space. If the α level for rejection were maintained at 0.05 for all comparisons (no Bonferroni correction used to guard against Type I error), 10 characters would have been considered significantly different between the species. However, the small differences in size between these characters further supports our conclusion that morphological differences between these species are subtle at best. In summary, visual inspection of these specimens failed to reveal a diagnostic character that reliably separates specimens of different haplotype lineages and no individual cranial or external measurement was adequate to separate animals of the two haplotypes.

Distance dendrograms based on 18 cranial measurements (Fig. 2) and 4 standard external body measurements (Fig. 3) of 53 independently identified *Eligmodontia* specimens yielded considerable mixing of specimens from different localities and also mixed specimens of known mtDNA haplotype into clusters with no apparent relationship to haplotype. An additional cluster analysis of these animals using only the characters that Braun (1993) regarded as useful in identifying species of *Eligmodontia* showed improved separation of the two species, but still did not match perfectly with the independent identifications (Fig. 4).

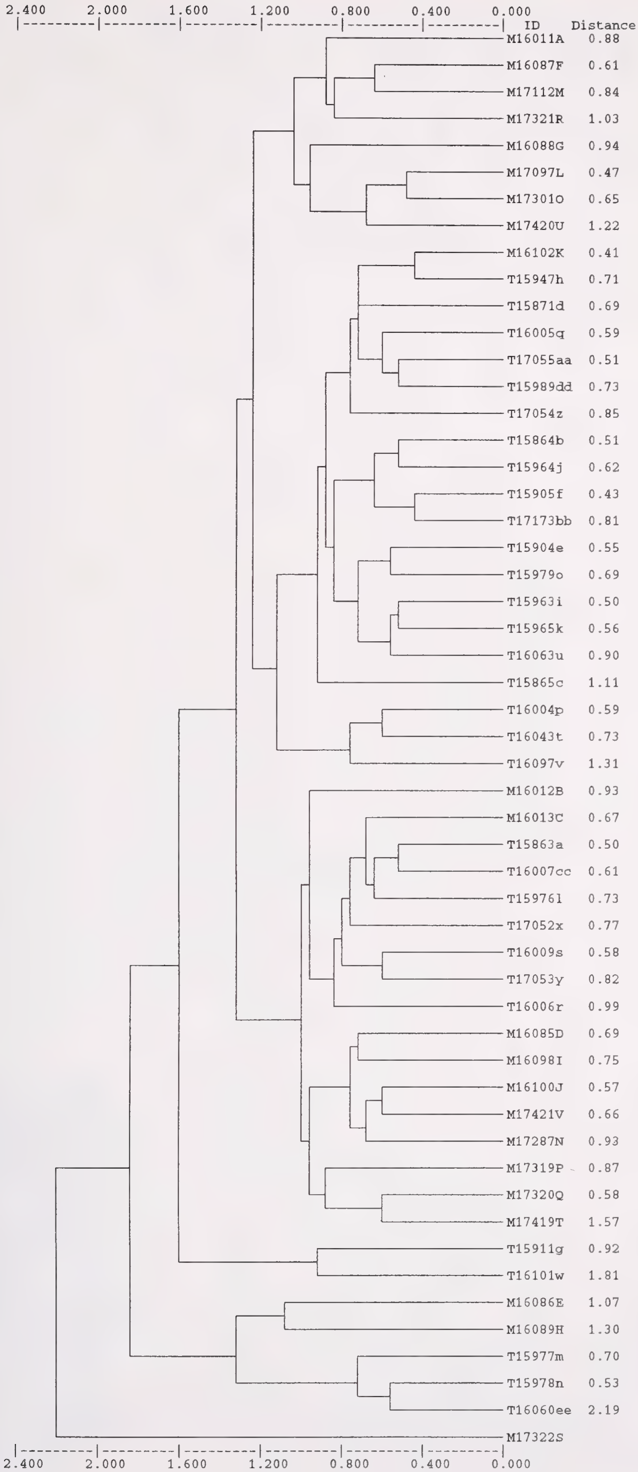
A discriminant function analysis based on all cranial measurements was 100% accurate in assigning independently identified individuals to the correct species. A similar analysis based only on the four external body measurements had an error rate of 3%; two *E. morgani* were classified as *E. typus.* The discriminant analysis using only Braun's (1993) characters resulted in an error rate of 6% and misidentified three *E. morgani* as *E. typus.* These analyses demonstrate that given these cranial characters and a sample of individuals of known species identity, the animals could be assigned reliably to the correct species only in multidimensional space.

Table 2. Specific trapping localities in Argentina and individual specimens of *Eligmodontia* captured at each locality that were identified by mtDNA, karyotype, or both. Individual character identification codes consist of a prefix indicating species (M = *E. morgani*, T = *E. typus*), MMNH specimen number, and suffix for cross-referencing individuals to Figs. 2–5.

Locality	Individuals
~15 km NE Mencué, 40°21.62′S, 69°31.59′W, Río Negro	M16085D, M16086E, M16087F, M16088G, M16089H
S Jose B. Casas, 40°33.25′S, 62°37.49′W, Buenos Aires	T17052x
~18 km SW Viedma, 40°56.41′S, 63°01.25′W, Río Negro	T17053y, T17054z, T17055aa
Arroyo La Fragua, 41°05.11′S, 70°57.26′W, Río Negro	M17419T, M17420U, M17421V
Tembrao, 41°10.19′S, 66°20.16′W, Río Negro	M17097L
Meseta de Somuncurá, 41°21.33′S, 67°55.69′W, Río Negro	T16097v, T16101w, M16098I, M16100J, M16102K
Istmo Ameghino, 42°25.8′S, 64°15.88′W, Chubut	T15963i, T15964j, T15965k, T16006r, T16009s, T16007cc
Caleta Valdés, 42°26.12′S, 67°55.69′W, Chubut	T15863a, T15864b, T15865c, T15871d, T16004p
Puerto Pirámide, 42°33.58′S, 64°15.88′W, Chubut	T159761, T15977m, T15978n, T15979o, T16060ee
Puerto Pirámide, 42°33.94′S, 64°17.27′W, Chubut	T16063u, T15989dd
~100 km W Dolavon, 43°17.14′S, 67°06.25′W, Chubut	T15947h
~30 km NW Pampa de Agnia, 43°28.78′S, 69°49.09′W, Chubut	T16043t
~27 km NW Pampa de Agnia, 43°29.74′S, 69°49.85′W, Chubut	M16011A, M16012B, M16013C
~200 km W Dolavon, 43°32.92′S, 68°07.78′W, Chubut	T15911g
~280 km W Dolavon, 43°45.30′S, 68°57.17′W, Chubut	T15904e, T15905f, T16005q
Ea. La Escondida, 45°19.39′S, 69°50.09′W, Chubut	M17319P, M17320Q, M17321R, M17322S
Meseta El Pedrero, 46°46.55′S, 69°37.59′W, Santa Cruz	T17173bb
Chile Chico, 46°53′S,70°56′W, Santa Cruz	M17112M
Ea. El Rincón, 46°56.35′S, 70°48.57′W, Santa Cruz	M17301O

►

Fig. 2. UPGMA distance dendrogram from cluster analysis based on 14 cranial characters of *Eligmodontia* representing 15 localities. The cophenetic correlation coefficient is 0.704. Identification labels are MMNH catalog numbers with a prefix indicating mtDNA species affiliation ("M" = *E. morgani*, "T" = *E. typus*). Character suffixes are used to cross-reference to individuals in Fig. 5 and Table 2.


2.400 2.000 1.600 1.200 0.800 0.400 0.000
ID Distance
M16011A 0.88
M16087F 0.61
M17112M 0.84
M17321R 1.03
M16088G 0.94
M17097L 0.47
M17301O 0.65
M17420U 1.22
M16102K 0.41
T15947h 0.71
T15871d 0.69
T16005q 0.59
T17055aa 0.51
T15989dd 0.73
T17054z 0.85
T15864b 0.51
T15964j 0.62
T15905f 0.43
T17173bb 0.81
T15904e 0.55
T15979o 0.69
T15963i 0.50
T15965k 0.56
T16063u 0.90
T15865c 1.11
T16004p 0.59
T16043t 0.73
T16097v 1.31
M16012B 0.93
M16013C 0.67
T15863a 0.50
T16007cc 0.61
T15976l 0.73
T17052x 0.77
T16009s 0.58
T17053y 0.82
T16006r 0.99
M16085D 0.69
M16098I 0.75
M16100J 0.57
M17421V 0.66
M17287N 0.93
M17319P 0.87
M17320Q 0.58
M17419T 1.57
T15911g 0.92
T16101w 1.81
M16086E 1.07
M16089H 1.30
T15977m 0.70
T15978n 0.53
T16060ee 2.19
M17322S
2.400 2.000 1.600 1.200 0.800 0.400 0.000

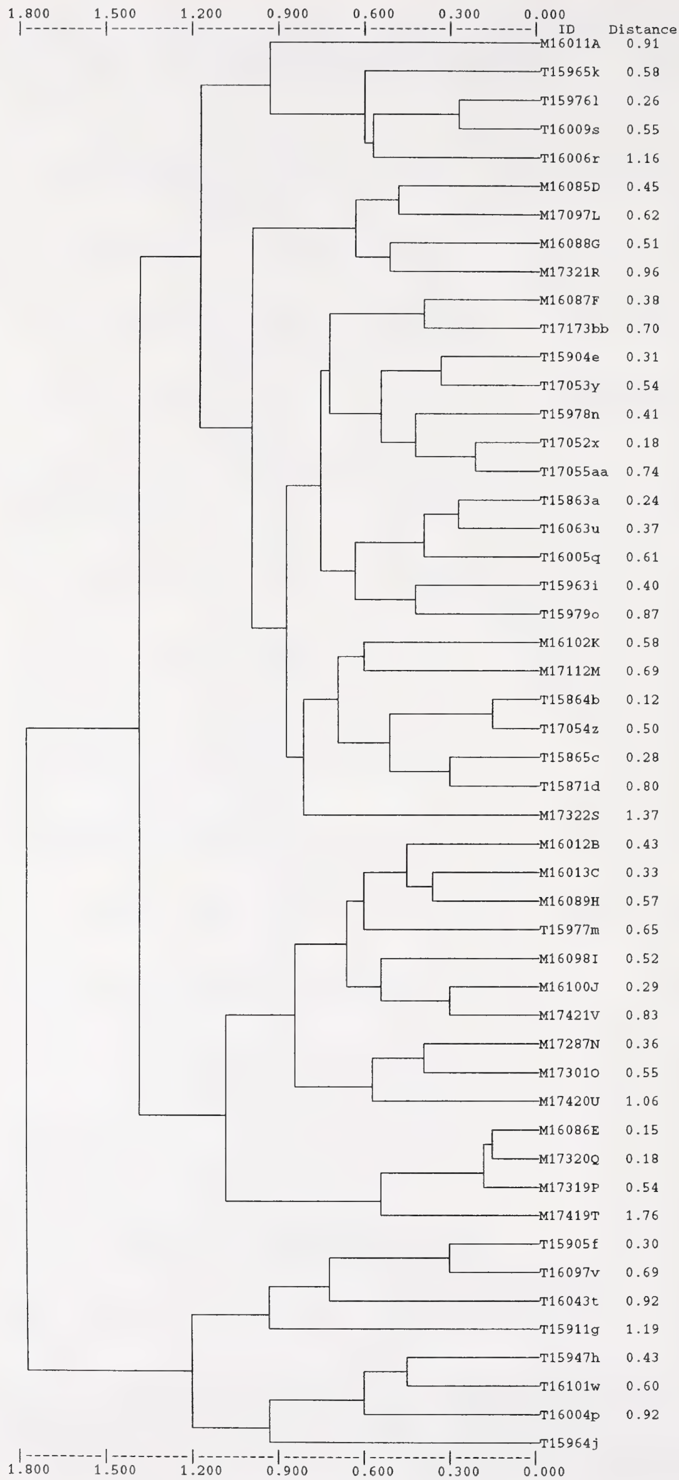


Fig. 3. UPGMA distance dendrogram from cluster analysis based on 4 standard external body measurements of *Eligmodontia* that showed mtDNA separation. The cophenetic correlation coefficient is 0.646. Identification labels are MMNH catalog numbers with a prefix indicating mtDNA species affiliation ("M" = *E. morgani*, "T" = *E. typus*). Character suffixes are used to cross-reference to individuals in Fig. 5 and Table 2.

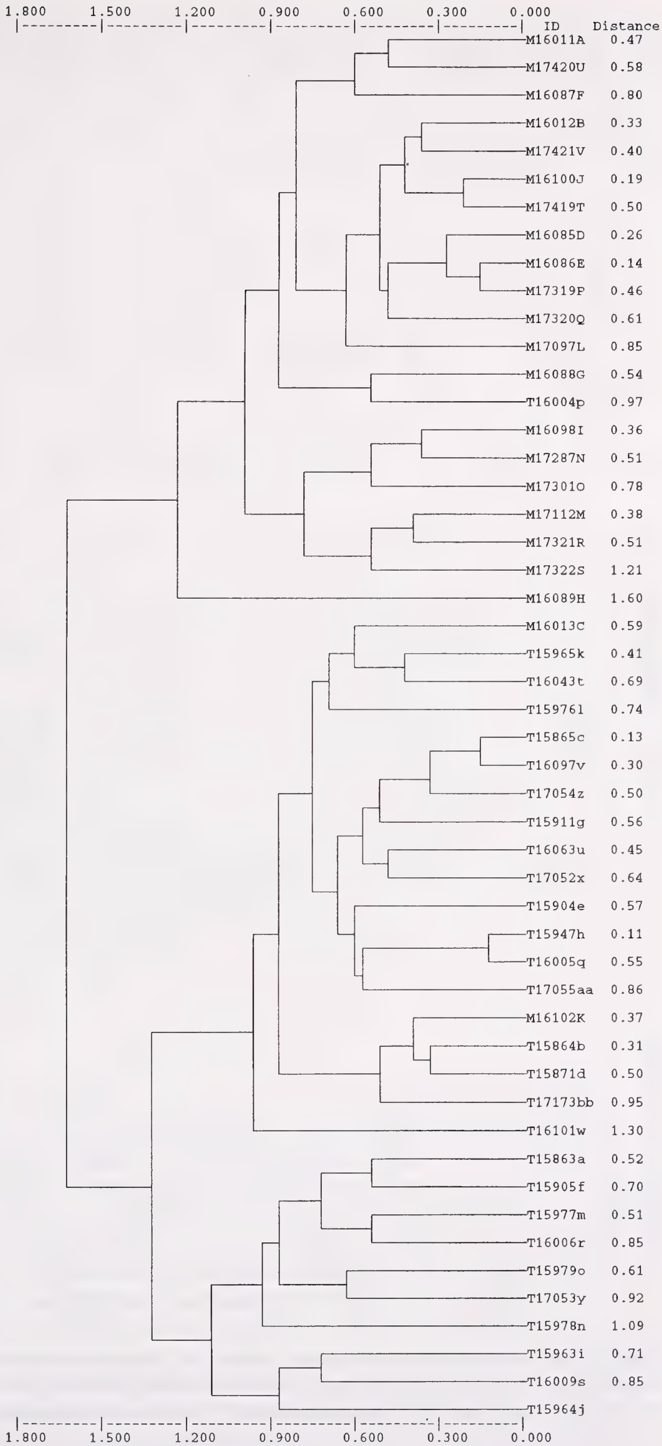


Fig. 4. UPGMA distance dendrogram from cluster analysis based on 5 characters (Braun 1993) of *Eligmodontia* that show mtDNA separation. The cophenetic correlation coefficient is 0.649. Identification labels are MMNH catalog numbers with a prefix indicating mtDNA species affiliation ("M" = *E. morgani*, "T" = *E. typus*). Character suffixes are used to crossreference to individuals in Fig. 5 and Table 2.

Step-wise discriminant function analyses allowed us to identify the characters with the strongest discriminating ability. Eight cranial characters met the admission criterion of the model. These characters were: 1) length of auditory bullae; 2) zygomatic breadth;

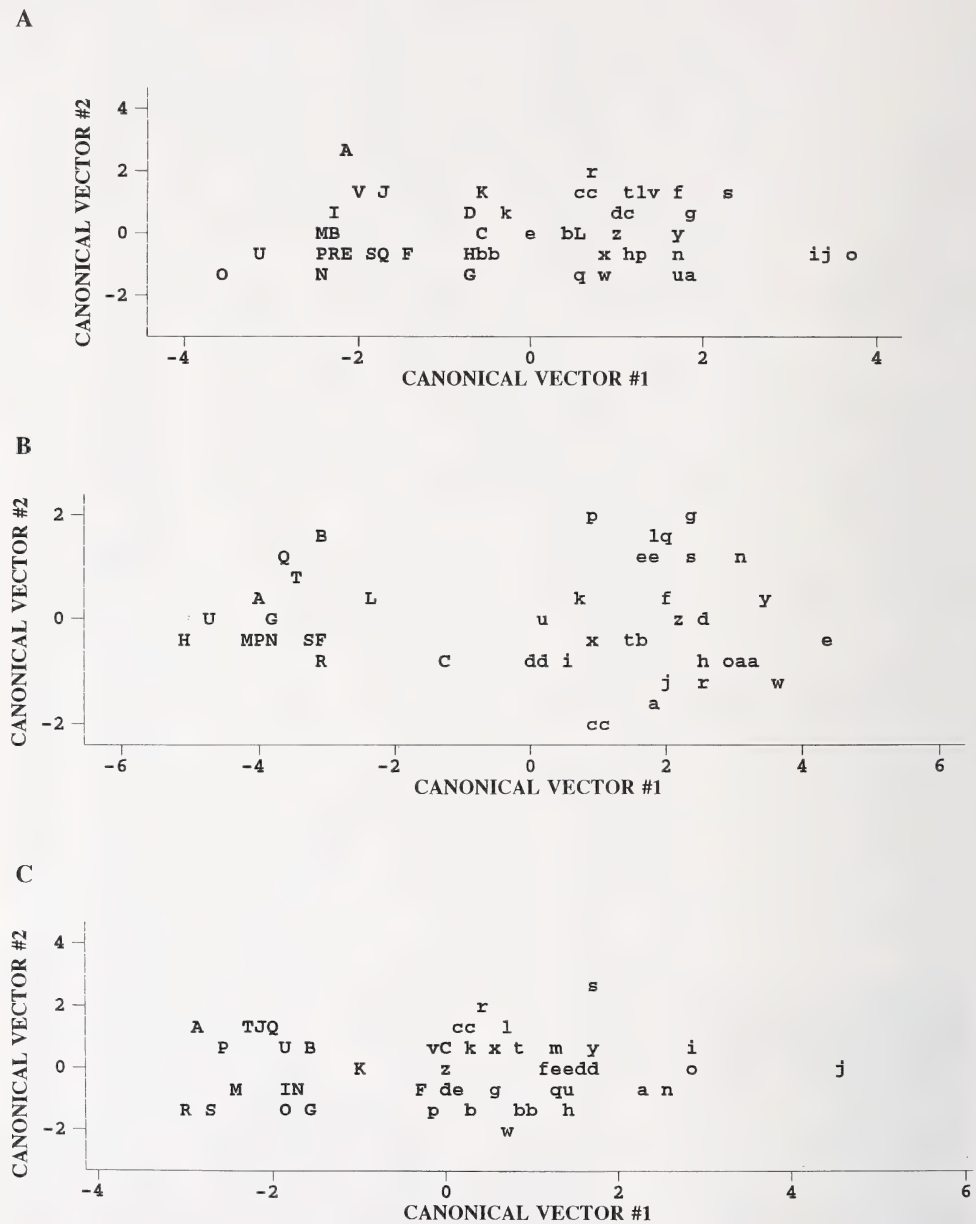


Fig. 5. Plots of canonical scores on first 2 canonical dimensions using those characters found to be significant discriminators by step-wise discriminant function analyses. A) external body measurements, B) cranial measurements, C) Braun's characters. Characters identify individuals with uppercase denoting *E. morgani* and lowercase denoting *E. typus*. Characters can be used to cross-reference individuals in Figs. 2–4 and Table 2.

3) breadth of auditory bullae; 4) length of palate; 5) length of maxillary toothrow; 6) greatest depth of skull; 7) mandibular length; and 8) length of incisive foramina. The three external characters that best distinguished between the species were: 1) tail length; 2) total length; and 3) length of the ear. Four of BRAUN's (1993) characters met the criterion for admission to the discriminant model. These characters were: 1) relative tail length; 2) relative length of the hind foot; 3) relative ear length; and 4) relative toothrow length. The step-wise discriminant function analysis eliminated only inflation of the auditory bullae in this last step.

Canonical discriminant function analysis reduced the dimensionality of the multivariate data set created in the step-wise discriminant function analysis (Fig. 5 a–c). When the data sets were considered separately, the combination of cranial characters proved most useful in assigning individuals to species. Results of the canonical discriminant function analysis of cranial characters showed that the first canonical dimension accounted for much of the variation ($R^2 = 0.88$). The species differed most widely in sums of the following linear combination: length of auditory bullae ×4.945 – zygomatic breadth ×1.552 – length of incisive foramen ×1.564 + breadth of auditory bullae ×4.080 + length of maxillary tooth row ×5.137 + mandibular height ×1.995 – length of palate ×2.270 + greatest depth af skull ×1.341.

Comparisons of the ability of the discriminant functions computed from specimens of known identity for each of the character sets to classify specimens of unknown identity showed that the combination of cranial characters was most useful. Ninety-three of 101 specimens (92.1%) were assigned to species with ≥95% probability of correct assignment using the discriminant function for cranial characters. In fact, 91 of 101 (90.1%) were classified with a probability ≥99.5%. However, a plot of specimens based on values computed from these same canonical coefficients did not show completely discrete clusters of individuals. In contrast, only 89 of 117 specimens (76.1%) and 76 of 103 specimens (73.8%), respectively, of unknown identity were assigned to species with ≥95% probability using data from external characters and BRAUN's (1993) characters. Despite the fact that the characters in each of these three data sets provided some discriminatory power when considered separately, when all of the characters were combined in an attempt to classify the unknowns, the number of individuals assigned to species with a probability ≥95% (82 of 88 specimens = 93.2%) was only slightly greater than results obtained using data on cranial characters alone. As in previous plots, there was no discrete clustering of specimens based in values computed from canonical coefficients.

Discussion

The original description of *Eligmodontia morgani* (ALLEN 1901) states that it is similar in color to *E. elegans* (now in the synonomy of *E. typus* – see MUSSER and CARLETON 1993), but has a smaller skull, shorter tail, and smaller ears. These characters were insufficient to assign our specimens unequivocally to species because there was overlap between individuals of known mtDNA haplotypes. Furthermore, despite the fact that significant differences were found between species in seven of the 18 morphological characters examined, specimens with independent identifications could not be classified correctly based on any single character. These results underscore the fact that single morphological characters and the ratios used by BRAUN (1993) are inadequate for reliable species identification. The fact that individuals from different localities and with different mtDNA haplotypes were mixed in our cluster analyses that were performed without regard to independent identifications further emphasizes the minimal degree of morphological divergence between these species. Although it should be noted that these analyses included individuals from 15 localities and included individuals of both sexes, our data indicate that there is lit-

tle or no sexual dimorphism in the morphological characters that we examined, so sex difference as a confounding factor was nonexistent or minimal. Our data set was insufficient to assess geographic variation within these species, but it is unlikely that "noise" introduced by geographic variation alone could inflate the within species variation to such an extent that between species variation was not detectable. Nevertheless, this is a potential that must be considered in future studies.

Only discriminant function analysis using cranial characters was able to identify correctly 100% of specimens of known mtDNA haplotypes as *E. typus* or *E. morgani*, so complete separation of the species based on morphology was possible only in multivariate character space. When specimens were plotted by canonical discriminant scores using only those characters found useful by the step-wise discriminant procedure, species did produce discrete clusters using eight cranial characters, less discrete clusters using Braun's (1993) ratios, and even less discrete clusters using standard external measurements. The linear combination of cranial characters, although not useful for field identification, should aid interested investigators in verifying the identity of museum specimens. Furthermore, the fact that specimens of unknown identity were assigned to species nearly as reliably based only on a combination of cranial characters as they were with a combination of all available characters suggests that a reduced data set consisting only of those characters found useful with step-wise discriminant function analysis is sufficient to identify most specimens. Despite the fact that we could not assign specimens reliably to species based on external characters, in handling adult animals in the field we sometimes had the general impression that adult individuals later identified as *E. morgani* on the basis of mtDNA haplotype were slightly smaller and more compact in body structure, with shorter ears and tails and softer pelage than those later identified as *E. typus*. This suggests that although external characters cannot be used to identify all specimens, they do provide some discriminatory power. These observations are consistent with the original description of *E. morgani* (Allen 1901).

Given the large difference in diploid chromosome numbers and the high degree of mtDNA divergence between these two groups, the position that they should be included under a single species name (Hershkovitz 1962) is clearly untenable (Ortells et al. 1989; Kelt et al. 1991; Zambelli et al. 1992; Braun 1993; Spotorno et al. 1994). However, the question of why they are so similar morphologically remains. Sympatric species that are reproductively isolated and that occupy similar niches generally are expected to diverge morphologically to minimize competition (Dayan et al. 1989, 1990; Grant and Schluter 1984; Malmquist 1985). We feel that there are at least three possible hypotheses for the lack of morphological divergence that warrant consideration: 1) interspecific hybridization; 2) recent, rapid divergence in mtDNA and karyotypes without differences in selective forces sufficient to cause morphological divergence; and 3) geographically widespread selective forces favoring a single phenotype within Patagonian populations of *Eligmodontia* that are affecting both species.

Introgressive hybrization could account for morphological similarity by the mixing of nuclear DNA. Given that mtDNA is inherited maternally and is not subject to recombination (Avise 1994), such hybridization would not obviate the presence of two distinct mtDNA lineages, which have been reported in mixed populations of *Canis lupus* × *Canis latrans* in North America (Wayne 1996). However, the amount of chromosomal divergence in *Eligmodontia* argues strongly against this hypothesis, suggesting instead that they are reproductively isolated (Kelt et al. 1991). None of the karyotypic studies to date has reported any specimen that was a potential hybrid. Finally, the fact that we were able to obtain discrete separation using discriminant function analysis supports the presence of at least two distinct species and provides no evidence of intermediate forms. On the basis of these considerations we feel that the hybridization hypothesis can be rejected.

Both of the remaining explanations depend on similarity of selective forces to main-

tain the low degree of morphological divergence between these species. Similarity of at least abiotic selective forces is likely in areas of sympatry, but *E. morgani* supposedly is confined to the western edge of the Argentine Patagonian region, whereas *E. typus* is considered to occur throughout central and eastern Patagonia (Kelt et al. 1991). Nevertheless, sympatry between these two has been documented previously. Zambelli et al. (1992) reported both the 2n = 44 and 2n = 32–33–34 karyotypes (= *E. typus* and *E. morgani*, respectively) at two localities in northern Patagonia–Junín de los Andes (Neuquén Province) and Los Menucos (Río Negro Province). Our data extend the distribution of *E. morgani* further eastward than previously was recorded and document additional localities of sympatry (Hillyard et al. 1997). Furthermore, because identification of many putative distributional records for these species was based on morphology alone without the benefit of a comparison data set to verify identity, or worse, solely on geographic location, the accuracy of most identifications is subject to verification and thus we really do not know distributional limits or degree of sympatry between the two species at this time. Nevertheless, the fact that even specimens from disparate localities show an extremely high degree of morphological similarity suggests either that the chromosomal and molecular divergence has been relatively recent and quite rapid (hypothesis 2) or that the primary selective forces influencing morphology are widespread and uniform (hypothesis 3).

Given the amount of mtDNA divergence reported by Hillyard et al. (1997) and using the most conservative rate of divergence discussed by Smith and Patton (1993), one can estimate that the separation between these two species occurred between 2.5 and 3 million years before the present (Pliocene or early Pleistocene). However, the available fossils of phyllotine rodents such as *Auliscomys*, *Graomys*, and *Reithrodon* dating from 2–3 mybp show little difference in comparison with modern specimens of the same genera (Reig 1978). The chromosomal differences observed in *Eligmodontia* are substantial and appear to have involved much more than simple chromosomal fissions and fusions (Ortells et al. 1989). Furthermore, the magnitude of mtDNA divergence between these two species is greater than typically is seen at the species level (Avise 1994). We can think of no reason why the rate of mtDNA divergence in *Eligmodontia* should be greater than in other rodent species. Collectively, because the fossil data support an early adaptive radiation of the Phyllotini and little morphological change in the intervening time, and because the magnitude of chromosomal and mtDNA differences is substantial, the hypothesis of rapid recent molecular and chromosomal divergence to explain differences between these species, although not fully falsified, seems unlikely.

If *E. morgani* and *E. typus* had non-overlapping distributions and selective forces influencing morphology of these species were consistent across both of their ranges, then extreme morphological similarity would not be surprising. However, in areas of sympatry this degree of morphological similarity would be expected to result in strong interspecific competition favoring character divergence (Dayan et al. 1989, 1990; Grant and Schluter 1984; Malmquist 1985). Although the biogeographic history of the two species is unclear, the genetic data available (Hillyard et al. 1997) and the present (albeit incomplete) distribution maps of these species suggest that they are sympatric in only a small portion of their present ranges. Historically, however, the two species might have interacted ecologically in interdigitating patches of Oriental (*typus*) and Occidental (*morgani*) landscapes as the two waxed and waned with changing temperature and precipitation as envisioned by Hillyard et al. (1997). Even if this hypothesis is correct, however, the total geographic ranges of the two species are largely allopatric and probably have been so for a very long time. Consequently, competition leading to character divergence probably has not been a major factor in their evolutionary history. Nevertheless, the evidence of past and present sympatry raises important ecological questions that now must be addressed concerning mechanisms of coexistence in these areas. How are mice of the two morphologically simi-

lar species partitioning available resources to minimize competition? To address this question we must first obtain better data concerning the distribution and microhabitat use of both species. By using the morphological data from our specimens as a "training" data set, it is possible to assign specimens of unknown or questionable species affiliation now in systematic collections to species with a high degree of reliability. These data will enable researchers to re-assess identification of existing specimens, better define species ranges, identify environmental features correlated with each species' distribution, and verify areas of presumed allopatry and sympatry. With these types of data in hand we can begin to evaluate species specific habitat requirements and assess how these congeners partition habitat space and resources.

There is no question that the Patagonian region supports at least two species of *Eligmodontia*, but their distribution and habitat requirements are poorly understood. *Eligmodontia* presents an evolutionary and ecological puzzle. SPOTORNO et al. (1994) suggested that the high degree of chromosomal divergence among the species of this genus might have resulted from isolation by both geographic (extrinsic) and chromosomal (intrinsic) factors. Our data regarding the morphological similarity between these species suggest that if they arose allopatrically the selective regimes affecting them either were too weak or too similar to produce much morphological divergence.

Acknowledgements

This work was funded in part by grants to ECB from the Graduate School, University of Minnesota, and NIH grant GM42563 to CJP and D. E. PUMO. CONICET and Universidad Nacional del Comahue provided salaries for Argentine investigators and provided local assistance. CONICET also provided funds to JAM for a two-year fellowship to work with these materials in the US. Travel expenses for CJP were provided by HCLAS grants from Hofstra University. Housing while we were in Puerto Madryn was provided by Centro Nacional Patagónico. Collecting permits were issued to ECB and JAM by Administración de Parques Nacionales, Argentina, Secretaría de Turismo de Chubut, and Dirección de Fauna y Flora Silvestres. Thanks to our field colleagues, botanists LUCIANA GHERMANDI and LAURA MARGUTTI and mammalogists NADIA GUTHMANN and SOFÍA HEINONEN FORTABAT, and to JAN DECHER for preparing the Zusammenfassung.

Zusammenfassung

Morphologische, chromosomale und molekulargenetische Divergenz bei zwei Arten von Eligmodontia

Karyologische Befunde und Untersuchungen der mt-DNA sprechen für das Vorhandensein von mindestens zwei verschiedenen Arten von *Eligmodontia* im argentinischen Patagonien. Die bisher vorhandenen morphologischen Daten reichen jedoch nicht aus, um die Individuen der beiden Arten verläßlich voneinander zu unterscheiden. In der vorliegenden Arbeit wurden an Stichproben von *Eligmodontia* aus 15 Herkünften in Patagonien morphologische Untersuchungen (äußere Körpermerkmale, Schädelmerkmale) durchgeführt. Mittels uni- und multivariater Analysen der Meßwerte wurde die Hypothese getestet, daß die vermuteten Arten *Eligmodontia typus* und *E. morgani* auch morphologisch voneinander verschieden sind. Von den einzelnen morphologischen Merkmalen erwies sich nach einem Vergleich mit chromosomalen und mtDNA-Daten keines als differentialdiagnostisch. Mittels Diskriminanzanalysen konnten die jeweiligen Individuen jedoch zuverlässig der einen oder anderen, aufgrund unabhängiger Daten postulierten Arten zugeordnet werden. Auf verschiedene Kombinationen von morphologischen Merkmalen gestützte Clusteranalysen zeigten einige Übereinstimmung mit den chromosomalen und molekularen Datensätzen. Individuen eines bestimmten mtDNA- Haplotyps bildeten jedoch nicht immer eine einheitliche Gruppe. Obwohl es bei *Eligmodontia* in Patagonien deutliche molekulare und karyologische Unterschiede gibt, werden diese nicht unbedingt von einer entsprechenden morphologischen Divergenz begleitet.

References

Allen, J. A. (1901): New South American Muridae and a new Metachirus. Bull. Amer. Mus. Nat. Hist. **14**, 405–412.

Avise, J. C. (1994): Molecular Markers, Natural History and Evolution. New York: Chapman and Hall.

Braun, J. E. (1993): Systematic relationships of the tribe Phyllotini (Muridae: Sigmondotinae) of South America. Spec. Publ. Oklahoma Mus. Nat. Hist.

Dayan, T.; Simberloff, D.; Tchernov, E.; Yom-Tov, Y. (1989): Inter- and intraspectific character displacement in mustelids. Ecology **70**, 1526–1539.

– (1990): Feline canines: community wide character displacement among the small cats of Israel. Amer. Nat. **136**, 39–60.

Engstrom, M. D.; Choate, J. R.; Genoways, H. H. (1994): Taxonomy. In: Seventy-five Years of Mammalogy (1919–1994). Ed. by E. C. Birney and J. R. Choate. Special publications No. 11. The American Society of Mammalogists. Pp. 179–199.

Grant, P.; Schluter, D. (1984): Interspecific competition inferred from patterns of guild structure. In: Ecological communities. Conceptual issues and the evidence. Ed. by D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle. Princeton, New Jersey: Princeton University Press. Pp. 201–233.

Hershovitz, P. (1962): Evolution of neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zoology **46**, 1–524.

Hillyard, J. R.; Phillips, C. J.; Monjeau, J. A.; Birney, E. C.; Sikes, R. S. (1997): Mitochondrial DNA analysis of the silky desert mouse *Eligmodontia* in northern Patagonia. Z. Säugetierkunde (in press).

Kelt, D. A.; Palma, R. E.; Gallardo, M. H.; Cook, J. A. (1991): Chromosomal multiformity in *Eligmodontia* (Muridae, Sigmodontinae), and verification of the status of *E. morgani*. Z. Säugetierkunde **56**, 352–358.

Lee, M. R; Elder, F. F. (1980): Yeast stimulation of bone marrow mitosis for cytogenetic investigation. Cytogen. and Cell Gen. **26**, 36–40.

Malmquist, M. G. (1985): Character displacement and biogeography of the pygmy shrew in Northern Europe. Ecology **66**, 372–377.

Marshall, L. G. (1979): A model for paleobiogeography of South American cricetine rodents. Paleobiology **5**, 126–132.

Musser, G. G.; Carleton, M. D. (1993): Family Muridae. In: Mammal Species of the World: A Taxonomic and Geographic Reference. Ed. by D. E. Wilson and D. Reeder. Washington: Smithsonian Institition Press. Pp. 501–756.

Ortells, M. O.; Reig, O. A.; Wainberg, R. A.; Hurtado de Catalfo, G. E.; Gentile de Fronza, T. M. L. (1989): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae) II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*. Z. Säugetierkunde **54**, 129–140.

Patterson, B.; Pascual, R. (1972): The fossil mammalian fauna of South America. In: Evolution, Mammals, and Southern Continents. Ed. by A. F. Keast, F. C. Erk, and B. Glass. Albany, New York: State University of New York Press. Pp. 247–309.

Patton, J. L. (1967): Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia, Heteromyidae). J. Mammalogy **48**, 27–37.

Pearson, O. P.; Martin, S.; Bellati, J. (1987): Demography and reproduction of the silky desert mouse (*Eligmodontia*) in Argentina. Fieldiana Zool. **39**, 433–446.

Reig, O. A. (1978): Reodores cricétidos del Plioceno Superior de la Provincia de Buenos Aires (Argentina). Publicaciones del Museo Municipal de Ciencias Naturales de Mar del Plata "Lorenzo Scaglia" **2**, 164–190.

Rice, W. R. (1989): Analyzing tables of statistical tests. Evolution **43**, 223–225.

Rohlf, F. J.; Kishpaugh, J.; Kirk, D. (1982): Numerical taxonomy system of multivariate statistical programs. Stony Brook: State Univ. New York.

SAS Institute Inc. (1990): SAS user's guide: statistics, version 6: North Carolina: Carey.

Smith, M. F.; Patton, J. L. (1993): The diversification of South American murid rodents: evidence from mitochondrial DNA sequence data. Biol. J. Linnean Soc. **50**, 149–177.

Spotorno, A. E.; Sufan-Catalan, J.; Walker, L. I. (1994): Cytogenetic diversity and evolution of Andean species of *Eligmodontia* (Rodentia, Muridae). Z. Säugetierkunde **59**, 299–308.

Wayne, R. K. (1996): Conservation genetics in the Canidae. In: Conservation Genetics: Case Histories from Nature. Ed. by J. C. Avise and J. L. Hamrick. New York: Chapman and Hall. Pp. 75–118.

Zambelli, A.; Dyzenchauz, F.; Ramos, A.; de Rosa, N.; Wainberg, R.; Reig, O. A. (1992): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae) III. New data on the distribution and karyomorphs of the genus *Eligmodontia*. Z. Säugetierkunde **57**, 155–162.

Authors' addresses: R. S. Sikes and E. C. Birney, Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, 100 Ecology Building, St. Paul, Minnesota 55108 USA, J. A. Monjeau, Departamento de Ecología, Universidad Nacional del Comahue, CC. 1336, Bariloche, Río Negro, Argentina, C. J. Phillips and Jeanna R. Hillyard Department of Biology, Illinois State University, Normal, IL 61761 USA.

Z. Säugetierkunde **62** (1997) 281–292

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Mitochondrial DNA analysis and zoogeography of two species of silky desert mice, *Eligmodontia*, in Patagonia

By Jeanna R. Hillyard, C. J. Phillips, E. C. Birney, J. A. Monjeau, and R. S. Sikes

Department of Biological Sciences, Illinois State University, Normal, Illinois, USA, James Ford Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, Minnesota, USA, and Departamento de Ecología, Universidad Nacional del Comahue, Bariloche, Río Negro, Argentina

Receipt of Ms. 14. 11. 1996
Acceptance of Ms. 17. 03.1997

Abstract

Historically, silky desert mice of the genus *Eligmodontia* have presented mammalogists with a complex and somewhat vexing taxonomic problem. At various times silky desert mice have been assigned to several species or to only one or two species. Most recently karyological evidence has suggested the presence of at least two morphologically cryptic species, *E. morgani* and *E. typus* in Patagonia. To further elucidate this issue, we used a combination of karyological data and DNA sequences from the mitochondrial cytochrome b protein-coding gene to test the hypothesis that there are at least two genetically distinguishable and reproductively isolated species in Patagonia. By this means we showed that *E. morgani* and *E. typus* can be recognized readily by their karyotypes and mtDNA. In fact they exhibit more than 10% divergence in a 348-base pair region of cytochrome b. Within each species the mtDNA sequences enabled us to identify numerous maternal lineages. Results of PAUP analyses used to place these lineages in a geographic context suggested that the oldest lineage in the sample of each species was rare and occurred in the northwestern portion of the study area. Each species also was characterized by a common, geographically widespread "star" lineage. Typically, at each locality we found the star lineage and one or more local, related lineages. These data are consistent with a historical bottleneck, rapid expansion through the star lineage, and subsequent settling in and production of new lineages. The unequivocal identification of individuals based on mtDNA, not previously possible on the basis of morphology alone, allowed us to begin mapping distribution of these two largely allopatric species. The data suggest that *E. morgani* occurs in more mesic habitats, whereas *E. typus* occupies more arid areas mostly to the east of the range of *E. morgani*.

Introduction

Silky desert mice of the genus *Eligmodontia* are small phyllotine rodents that occur over a large geographic region encompassing western Bolivia, southern Peru, northern Chile, and Argentina. In general terms these mice are thought to inhabit arid scrubland habitats characterized by as little as 150–500 mm annual precipitation and at least some of the species are capable of using halophytic plants as a source of water (Mares 1977). However, detailed zoogeographic, ecological, and physiological studies of silky desert mice have been hampered by uncertainty as to species identifications and changing taxonomic arrangements. Presently, the ranges of putative species and their habitat requirements essentially are unknown.

The silky desert mice have had a complicated taxonomic history that dates back to early work by Phillipi (1896), Thomas (1916), and Allen (1901). More recently, Hershko-

VITZ (1962) lumped them into a single species (*E. typus*, as shown in REDFORD and EISENBERG 1992), whereas MUSSER and CARLETON (1993) recognized four species. For the most part, the confusion about *Eligmodontia* taxonomy can be traced to the facts that (a) sample sizes have been small and from widely scattered geographic locations and (b) traditional morphological features have failed to consistently delineate species (SIKES et al. 1997). The difficulties of working with *Eligmodontia* are especially evident in the Patagonian region of Argentina. In this region one could argue on morphological grounds (as HERSHKOVITZ did in 1962) that a single species occurs from the Andean foothills on the west to the arid Atlantic coast on the east. On the other hand, karyotypic analyses (including G- and C-banding) of specimens collected in various parts of Patagonia have revealed two distinctive cytotypes, one with a 2N= 43–44 karyotype and the other with 2N = 32–33. Based on geography, ORTELLS et al. (1989) concluded that the 2N = 43–44 karyotype was associated with *E. typus* and KELT et al. (1991) associated the 2N = 32–33 karyotype with *E. morgani* based on the fact the specimens with this arrangement were captured within 70 km of the likely type locality of this species (ALLEN 1901).

In contrast to morphological evidence and some taxonomic arrangements, the karyotypic evidence thus clearly indicates the existence of at least two reproductively isolated species of *Eligmodontia* in Patagonia. However, karyotypic data are not available for most museum specimens of *Eligmodontia* and research collections are incomplete in terms of geographic and ecological representation. Thus, in our overall investigation we sought to further elucidate the genetics of the two cytotypes, to expand the geographic and ecological representation of specimens that could be assigned reliably to reproductively isolated units labeled as *E. morgani* or *E. typus*, and use these animals to test more fully their morphological characteristics. In the present study we use mtDNA sequences and karyotypic data to evaluate genetic divergence between and within these species and to develop hypotheses concerning historical biogeography. These data provide new information on the distribution of the two species and document areas of sympatry. A second contribution (SIKES et al. 1997) contrasts morphological divergence with the patterns of karyotypic and genetic divergence presented herein.

Methods

Sixty-seven specimens of *Eligmodontia* were used in the present analyses. Voucher specimens of 66 of the mice were deposited in the collection of the James Ford Bell Museum of Natural History, University of Minnesota, St. Paul (MMNH specimen numbers). One animal (FMNH 133049) used in the study came from the Field Museum of Natural History, Chicago: it served as a cytotypic voucher from KELT et al. (1991) and represented *E. morgani*.

Mice were captured at 16 localities in Río Negro, Chubut, and Santa Cruz provinces (41° to 44° south latitude; 63° to 71° west longitude). Liver, kidney, and heart tissues were taken in the field and quick frozen and stored in liquid nitrogen. Chromosome spreads also were prepared in the field for selected specimens following the methods of PATTON (1967) as modified by LEE and ELDER (1980).

To obtain genetical data on Patagonian *Eligmodontia*, we elected to use DNA sequencing of a 348-base pair (bp) region of cytochrome b, which is a mitochondrial protein-coding gene. The tempo and mode of evolution differs among types of mitochondrial genes (PUMO et al. 1992), but cytochrome b is known to provide good resolution for inter- and even intra-specific geographic analyses of rodents and other kinds of mammals (e. g., SMITH and PATTON 1991; IRWIN et al. 1991). Given the rate of evolution in the cytochrome b gene (estimated at 2–4%/1×10^6 years, BROWN et al. 1979; MARTIN et al. 1992), we anticipated that reproductively isolated rodent species should exhibit differences in cytochrome b DNA sequences. Mitochondrial DNA (mtDNA) offers several advantages including the opportunity to compare the data set to those from other rodents and, possibly, to trace the zoogeographic history of species in a geographic region (AVISE 1994).

In the laboratory, total DNA was prepared from tissues by the proteinase K method (KOCHER et al. 1989). After extraction by phenol-chloroform-isoamyl alcohol, samples were subjected to the polymer-

ase chain reaction (PCR) using primers MVZ04 and MVZ05 designed for a region of the protein-coding cytochrome b gene in the mitochondrial genome (Smith and Patton 1991). Amplification (Saiki et al. 1985, 1988) was performed with Taq polymerase (Perkin-Elmer) for 30 cycles. Excess primer and nucleotides were removed from PCR products by using a GENECLEAN II kit (BIO 101) and following manufacturer's directions. Purified, amplified mtDNA was sequenced using Sequenase Version 2.0 (United States Biochemical) and [^{35}S]dATP or by means of an ABI-310 automatic sequencing system (Perkin-Elmer). Finally, DNA sequence alignment was performed with the IBI MacVector (version 4.1) software and phylogenetic analyses were done with PAUP v 3.0 (Swofford 1993). The mtDNA sequences have been submitted to GenBank.

Results

Our first step was to compare mtDNA sequence data from 15 specimens for which we also had karyotypic data. Our reference point was a mouse (2N = 32–33 cytotype) that previously had been assigned to *Eligmodontia morgani* on the basis of geographic origin (Kelt et al. 1991; FMNH 133049, Tab. 1). Mitochondrial DNA from this mouse was se-

Table 1. Collection localities and mtDNA lineages for the voucher specimens of *Eligmodontia* used in the combined DNA sequence and karyological analyses. Abbreviations: FMNH (Field Museum of Natural History number; specimen from study by Kelt et al. 1991); MMNH (James Ford Bell Museum of Natural History number).

Specimen number	Assigned mtDNA haplotype lineage	Species	Locality	
		Karyotype: 2N = 32–33: mtDNA Haplotype M		
FMNH 133049	M1	*E. morgani*	Ea. La Vizcaina	46°55′S, 70°50′W
MMNH 17097	M12	*E. morgani*	Tembrao	41°08.5′S, 66°18.5′W
MMNH 17112	M8	*E. morgani*	Chile Chico	46°33′S, 70°56′W
MMNH 17287	M3	*E. morgani*	Ea. El Rincón	46°59.8′S, 70°42.7′W
MMNH 17356	M3	*E. morgani*	La Subida	43°58.55′S, 70°22.97W
MMNH 17321	M10	*E. morgani*	Ea. La Escondida	45°19.4′S, 69°50.1′W
MMNH 17322	M9	*E. morgani*	Ea. La Escondida	45°19.4′S, 69°50.1′W
		Karyotype: 2N = 43–44: mtDNA Haplotype T		
MMNH 17052	T18	*E. typus*	Viedma	40°56.4′S, 63°01.3′W
MMNH 17053	T6	*E. typus*	Viedma	40°56.4′S, 63°01.3′W
MMNH 17054	T15	*E. typus*	Viedma	40°56.4′S, 63°01.3′W
MMNH 17055	T17	*E. typus*	Viedma	40°56.4′S, 63°01.3′W
MMNH 17056	T1	*E. typus*	Viedma	40°56.4′S, 63°01.3′W
MMNH 17087	T6	*E. typus*	Aguada Cecilio	40°51.49′S, 65°48.35′W
MMNH 17172	T14	*E. typus*	El Pedrero	46°48.1′S, 69°37.6′W
MMNH 17173	T19	*E. typus*	El Pedrero	46°48.1′S, 69°37.6′W

quenced and the cytochrome b sequence was labeled as the M haplotype. We next sequenced the remaining 14 animals. Six of these had karyotypes consistent in number and morphology with the specimen from the study by KELT et al. (1991). Although none had a cytochrome b sequence identical to the M haplotype, there were five new sequences (one shared by two mice) that differed from the M haplotype by only 1–6 nucleotide bases. Thus, these six animals (including two that had been obtained within 40 km of the type locality of *E. morgani*) were identified as *E. morgani* and the five mtDNA sequences (one shared, Tab. 1) were labeled numerically as "lineages" of the M haplotype (M12, M8, M3, M10, M9). The reference animal (FMNH 133049) was labeled M1. Eight animals were assigned to *E. typus* on the basis of having karyotypes consistent with that described for the species (2N = 43–44) by ORTELLS et al. (1989). The mtDNA cytochrome b sequences from these animals differed markedly from all six lineages in the *E. morgani* M haplotype. Indeed, among the animals assigned to *E. typus* on basis of karyotype, their mtDNA sequences typically differed from the M haplotype lineages by more than 34 nucleotide bases (>10% sequence difference) and were designated as representing the T haplotype. Among the specimens of *E. typus*, there were seven different mtDNA sequences differing by 1–6 nucleotide bases. These were labeled numerically as T1, T6, T14, T15, T17, T18, and T19 (Tab. 1). Collectively, the lineages of the M and T haplotypes from animals of known karyotype were analyzed by means of PAUP and the two groups of mtDNA lineages formed two clades in complete congruence with the chromosomal data (Fig. 1).

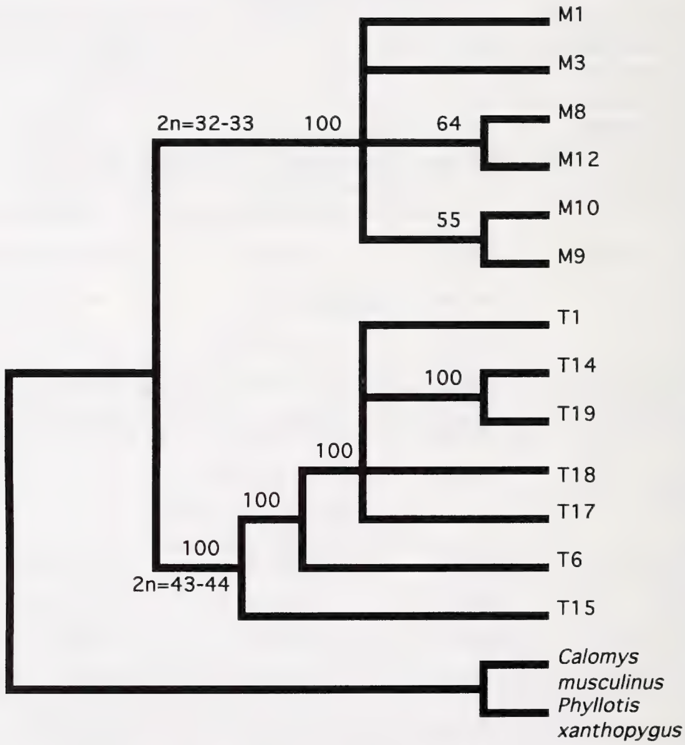


Fig. 1. Fifty percent majority rule consensus PAUP tree with analysis (100 iterations) of the 348-bp region of cytochrome b of two species of *Eligmodontia*. Bootstrap values are shown above each branch. The diploid chromosomal number is listed for each clade. Homologous DNA sequences from two genera of Patagonian rodents, *Phyllotis xanthopygus* and *Calomys musculinus*, were used as outgroups. The tree length is 152 steps, the consistency index is 0.836, and the retention index is 0.896.

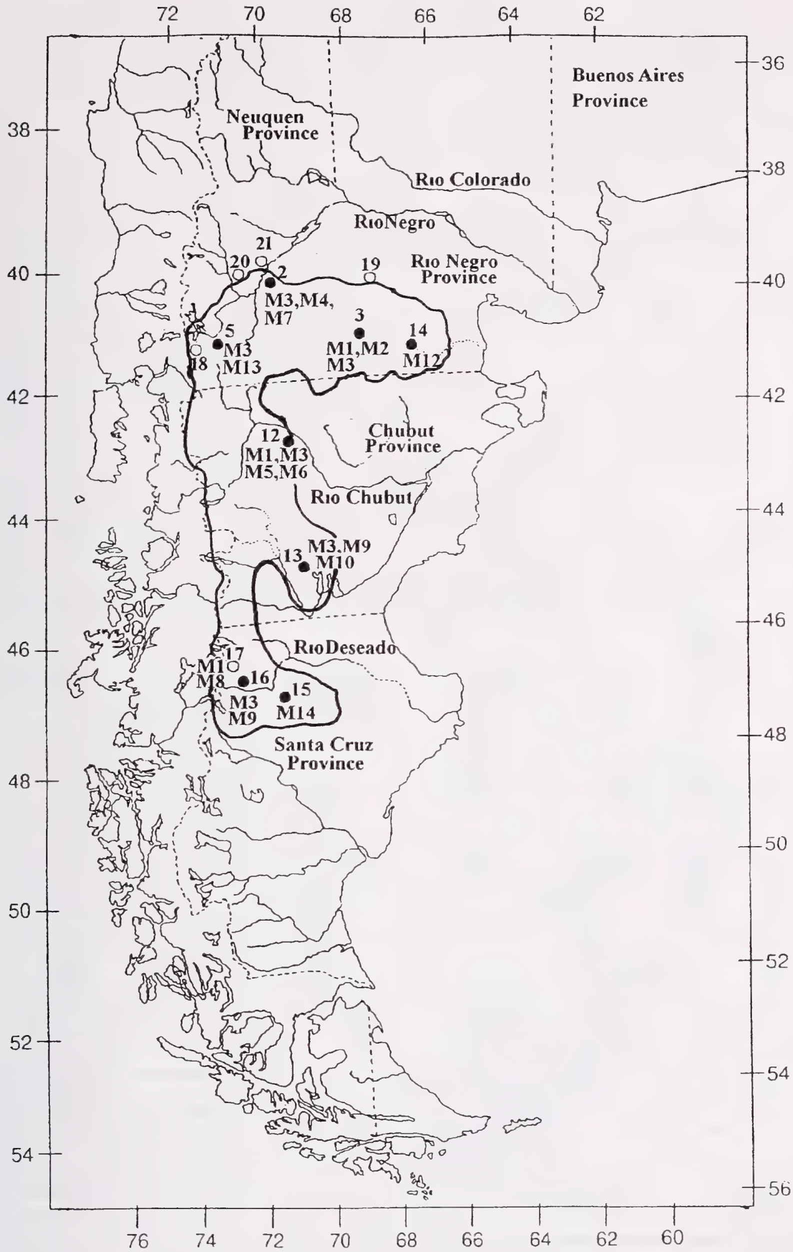


Fig. 2. Localities of *Eligmodontia morgani* in Río Negro, Chubut, and Santa Cruz provinces of Argentina (confirmed by chromosomal, mtDNA data, or both). Open circles indicate localities from ORTELLS et al. (1989) and KELT et al. (1991). The closed circles are localities for specimens examined in the present study. MtDNA haplotypes are listed next to collection localities. The solid line shows an area known as the Extra-Andean Occidental Megabiozone (DEL VALLE et al. 1995).

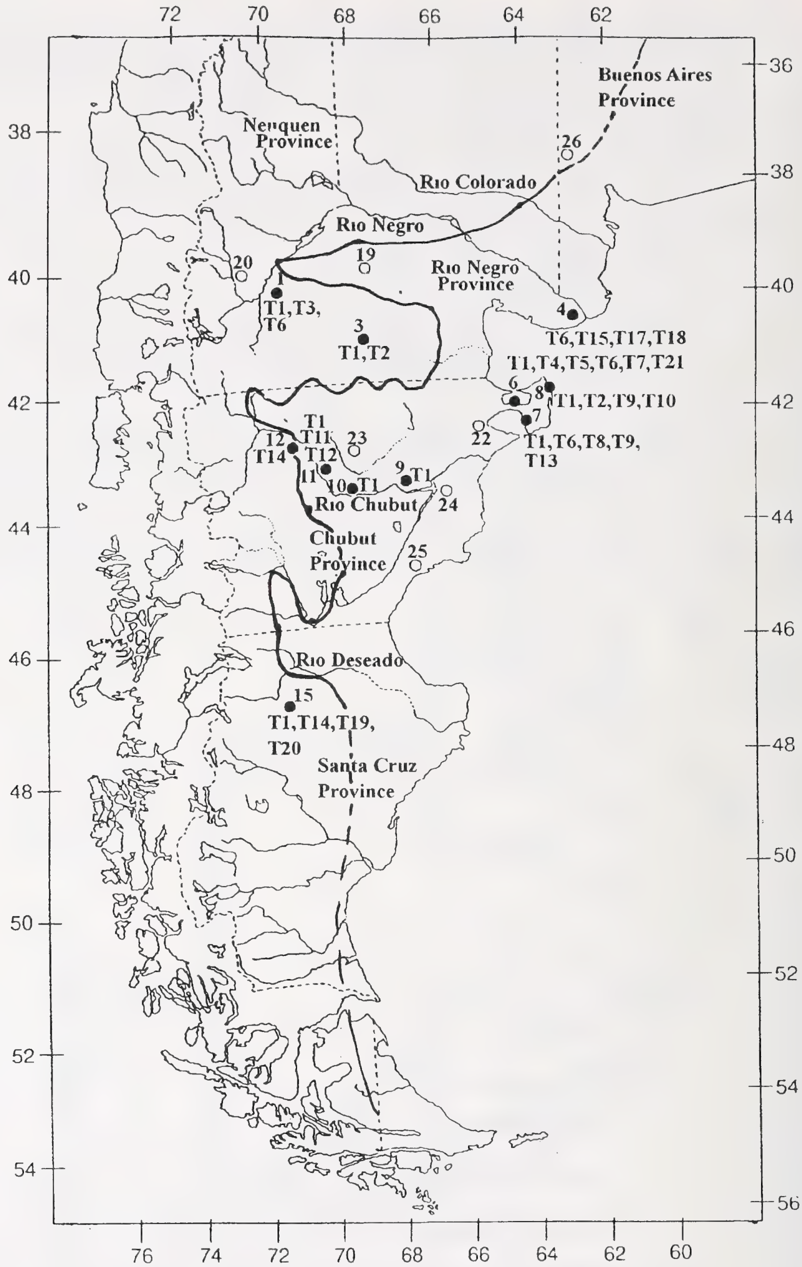
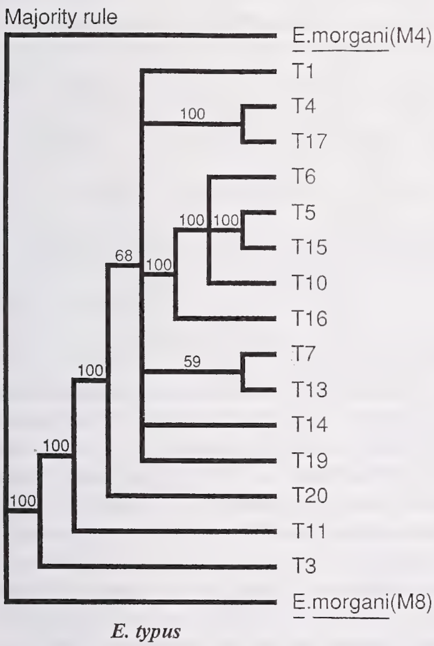


Fig. 3. Localities of *Eligmodontia typus* in Buenos Aires, Neuquen, Río Negro, Chubut, and Santa Cruz provinces of Argentina (confirmed by chromosomal, mtDNA data, or both). Open circles indicate localities of specimens from ORTELLS et al. (1989), KELT et al. (1991), and ZAMBELLI et al. (1992). The closed circles are localities for specimens examined in the present study. MtDNA lineages are listed next to collection localities. The solid line coincides with an area known as the Extra-Andean Oriental Megabiozone (DEL VALLE et al. 1995). The dashed lines estimate the continuation of this vegetation type and our distributional hypothesis for *E. typus* outside the boundaries of this study area.

The second part of our investigation involved sequencing the same region of the cytochrome b gene in the remaining 52 "unknown" specimens (i. e., no karyotypic data) and using a PAUP analysis to assign each animal to a species based on its mtDNA. As a result, we had a total sample of 36 specimens of *E. typus* from 11 localities. Within the total sample for this species, there were T21 haplotype lineages that differed by as many as 9 bases (2.6%). The total sample of *E. morgani* was 28 animals from 10 localities. In this sample there were 14 M haplotype lineages that diverged by as much as 2.3%.

In terms of the molecular evolution of the cytochrome b gene we found a striking difference between the two species. In *Eligmodontia typus* we found 38 variable positions in the T haplotype: 79% of these were third position C–T transitions; 15.8% were third position A–G transitions; and the remaining two were first and third position transversions, giving a transition : transversion ratio of 14 : 1. Although the total divergence within the *E. morgani* M haplotype was similar to that in the T haplotype, the pattern of molecular evolution was different. In the M haplotype we found 23 variable positions: 43% of the substitutions were third position C–T transitions; 21.7% were third position A–G transitions; and the remaining substitutions either were first or second position transitions or were transversions (the latter being 21.7% of the total number of substitutions, giving a transition : transversion ratio of only 4 : 1).

For a phylogeographic and historical perspective based on mtDNA sequences we undertook PAUP analyses for each species (Figs. 4, 5). In each case we used two of the mtDNA lineages from one species to polarize the lineage tree for the other species. No strong evidence of geographic structuring was evident in either species. That is, no clades



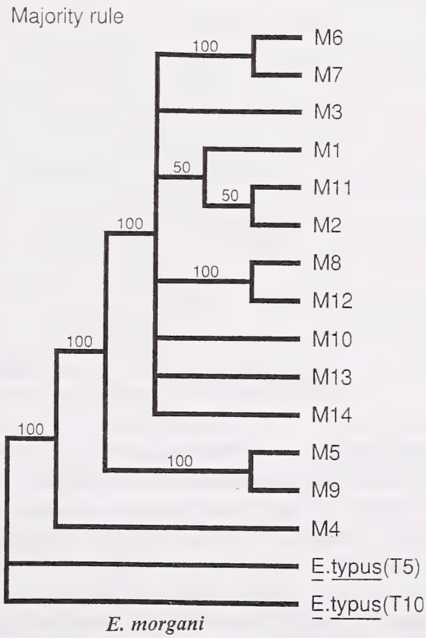


Fig. 4. Majority rule consensus PAUP tree with bootstrap analysis (100 iterations) of 15 mtDNA haplotypes of *Eligmodontia typus* using sequences from *Eligmodontia morgani* as outgroups. Bootstrap values are shown above each branch.

Fig. 5. Majority rule consensus PAUP tree with bootstrap analysis (100 iterations) of 14 mtDNA haplotypes of *Eligmodontia morgani* using sequences from *Eligmodontia typus* as outgroups. Bootstrap values are shown above each branch.

of lineages in either species could be identified as "characteristic" of a specific geographic area (Figs. 4, 5). In each species one particular lineage predominated in terms of numbers of animals and geographic distribution: in *E. morgani* 12 mice (43%) represented the M3 maternal lineage, which was found at six localities as much as 700 km apart; in *E. typus*, 10 mice (28%) represented the T1 lineage, which was obtained all but one locality where the species was found (Fig. 2). Polarization of the PAUP tree enabled us to hypothesize the basal lineage(s) among all of the M and T haplotype lineages. In *E. morgani*, the M4 lineage, obtained at a locality near Mencué in northwestern Río Negro Province, was hypothesized as the oldest extant lineage in our sample (Fig. 4). In *E. typus*, the T3 lineage from Ea. María Sofía in northwestern Río Negro Province (<70 km from the Mencué locality) was hypothesized by the PAUP analysis as the extant basal lineage in the sample (Fig. 4). In both species these basal lineages were rare (isolated from a single animal).

Discussion

Although silky desert mice of the genus *Eligmodontia* in Patagonia show little morphological divergence (Hershkovitz 1962; Sikes et al. 1997), recent karyological studies by Ortells et al. (1989), Kelt et al. (1991), and Zambelli et al. (1992) clearly established the existence of at least two karyological cytotypes in the region. Moreover, because it is highly improbable that animals with 2N = 32–33 and 2N = 43–44 chromosomal arrangements could interbreed successfully (see also Kelt et al. 1991), it also can be concluded that the cytotypes are reproductively isolated. Our mtDNA data are fully congruent with the chromosomal data and the absence of shared haplotypes, or lineages, between cytotypes supports the logical conclusion of reproductive isolation between *E. morgani* and *E. typus*.

Collectively, the karyological and mtDNA data can be used to shed some light on the likely history of *E. morgani* and *E. typus*. Insofar as chromosomal divergence is concerned, the difference between these two species presently appears to be a combination of small Robertsonian rearrangements and an array of pericentric inversions, tandem translocations, and, probably, euchromatic amplifications and deletions (Ortells et al. 1989). From this one might infer that chromosomal differences accumulated over time, perhaps after the parent metapopulation had been physically subdivided. Alternatively, there might have been an initial event that resulted in reproductive isolation or limited fertility between cytotypes within a population. In terms of the mtDNA data, the difference between the M and T haplotypes (>10%) seems to suggest a relatively old divergence. Presently there is no way to calibrate the rate of molecular evolution of cytochrome b in *Eligmodontia*, but an application of generalized rate in mammals (Brown et al. 1979; Martin et al. 1992) would imply a coalescence of the two haplotypes in the early Pleistocene or late Pliocene. More importantly, the divergence between the M and T haplotypes is far greater than the divergence within each (>10% vs <2.6%) and, thus, the historical starting point for the two haplotypes considerably predates the origins of any of the known extant lineages. A deep history of divergence could be indicative of an early, rapidly occurring physical split in the parent population (from geographic or chromosomal causes) as opposed to a speciation process that was (a) recent, (b) gradual, or (c) characterized by periodic hybridization (Lehman et al. 1991; Hughes and Carr 1993). Finally, it should be noted that the foregoing interpretation is not reflected in the morphology of these mice. The striking physical similarity between the two species, which caused the original taxonomic complications, belies their dramatic genetic and karyotypic difference. This similarity raises additional questions about the history of the species and the selection pressures they have experienced (Sikes et al. 1997).

The mtDNA lineages in our samples of both *E. morgani* and *E. typus* that were hypothesized as being the oldest were found in northwestern Patagonia. In both species

these old lineages appear to be rare (isolated from single animals), but this is what one might expect because of stochastic lineage extinction (Moritz 1994; Avise 1996). The geographic positioning of old lineages could be misleading because other, older, lineages might be uncovered by additional sampling. However, it also is possible that our data are indicative of the geographic source of the modern population of each species (Avise 1996). For example, the hypothesized oldest lineage in our sample of *E. morgani* (M4) was found in northwestern Río Negro Province rather than in the southern or eastern part of the present range (Fig. 2). From this information we could hypothesize that the modern Patagonian population of *E. morgani* originated somewhere in the steppe-like habitats east of the Andes in northwestern Patagonia (c. f. the Extra-Andean Occidental biozone of del Valle et al. 1995). The data for *E. typus* are interesting because although the species presently is abundant along the Atlantic coast, the hypothesized basal lineage (T3) was found in northwestern Patagonia. So, although we had anticipated that the *E. typus* population might be traced to the Atlantic coastal region north of Patagonia, the mtDNA data seem to imply that the modern Patagonian population of *E. typus* was derived from the west rather than the coastal region. This interpretation would suggest that modern populations of both *E. typus* and *E. morgani* trace to the same general geographic region. Although it is possible that both survived the end of the Pleistocene in a refugium in the eastern shadow of the Andes, this conclusion is limited by the geographic scope of our study. For example, *E. typus* also occurs well to the northeast of our region and we presently have no mtDNA data from there. Thus, the potential hypothesis that the two species shared a refugial zone is speculative until additional specimens are collected both north and south of our present study area.

It also should be noted that our data set is unusual in that the hypothesized basal lineages in both species were found in only a single locality and represented by a single individual in our sample. Sometimes, basal lineages are the most common and geographically widespread within a species (Crandall and Templeton 1993) but a pattern similar to the one seen in *Eligmodontia* also has been observed in the Jamaican fruit bat, *Artibeus jamaicensis*. In this instance a derived lineage occurs from the Yucatán Peninsula of México through the Caribbean, whereas basal lineages are found only on the mainland or individual islands (Phillips et al. 1991). Additionally, it should be noted that our data overall are similar to phylogeographic mtDNA data from other species of vertebrates (Avise 1987) and this might reflect a common post-Pleistocene phenomenon of rapid range expansion.

Beyond the geographic polarity described above, the PAUP analyses did not reveal any geographic structuring in the distribution of the mtDNA lineages. Thus, within the limits of genetic resolution provided by the cytochrome b sequences there is no indication that animals in some portion of the studied species ranges have been isolated for long periods of time. In fact, in each species there is a particular lineage (T1 and M3) represented at virtually every locality sampled (Figs. 2, 3). The pattern of one common, widespread, lineage with numerous associated local lineages that could be derived from it by a small number of nucleotide base substitutions, as observed in both species in our study, has been referred to as a star lineage. Our tentative interpretation is that both *E. typus* and *E. morgani* experienced population bottlenecks and then underwent population expansions and spread fairly quickly into their current ranges.

It is reasonable to imagine these bottlenecks occurring in northwestern Patagonia where we found the hypothesized oldest lineage of each because this is a region where the Oriental (occupied primarily by *E. typus*) and Occidental (occupied primarily by *E. morgani*) biozones interdigitate with one another depending on elevation (Monjeau et al. in press). During glacial retreats and advances of the Pleistocene (Clapperton 1993) there would have been alternating episodic expansions and contractions of these biozones caused by climatic changes and these would have resulted in the development of small

isolated patches of first one and then the other habitat type, and hence small populations of first one and then the other species of *Eligmodontia*. Such small populations are the bottlenecks we envisage. The present day legacy of this history may be greater for *E. morgani* than for *E. typus* because the latter species has a much broader overall distribution. Although this interpretation of our data is consistent with the landscape history of this region, other interpretations are possible and ours requires further testing.

The genetic delineation of these two species of silky desert mice further our understanding of their respective distributions in Patagonia. Our data, based on specimens for which unequivocal identifications are available, largely corroborate the conclusions of Kelt et al. (1991) that *E. morgani* is more restricted to western Patagonia, whereas *E. typus* occurs broadly throughout the central and eastern portions of Patagonia (Figs. 2, 3). However, these data do extend the known distributions of *E. morgani* further eastward than previously known. The distributions of these species in Patagonia appear to follow the Megabiozones described for this area by del Valle et al. (1995) with *E. typus* occurring primarily in the Extra-Andean Oriental biozone and *E. morgani* primarily in the Extra-Andean Occidental biozone (Monjeau et al. in press). At most localities we captured one species or the other, but we caught both species within walking distance of our camps at three ecotonal localities – Meseta de Somuncura, Ea. Mallín Blanco north of Pampa de Agnia, and Meseta El Pedrero. These data corroborate the earlier report by Zambelli et al. (1992) that these morphologically cryptic species sometimes are sympatric.

The data presented herein document substantial genetic divergence between *E. morgani* and *E. typus* that is in sharp contrast to their high degree of morphological similarity. The patterns of intraspecific genetic divergence pose questions concerning patterns of gene flow and lineage divergence on a local scale, but the deep divergence between the T and M haplotypes raises questions concerning their respective biogeographic histories.

Acknowledgements

This work was funded in part by grants to ECB from the Graduate School, University of Minnesota, and NIH grant GM42563 to CJP and D. E. Pumo. CONICET and Universidad Nacional del Comahue provided salaries for Argentine investigators and provided local assistance. CONICET also provided funds to JAM for a two-year fellowship to work with these materials in the US. Travel expenses for CJP were provided by HCLAS grants from Hofstra University. Housing while we were in Puerto Madryn was provided by Centro Nacional Patagónico. Collecting permits were issued to ECB and JAM by Administración de Parques Nacionales, Argentina, Secretaría de Turismo de Chubut, and Dirección de Fauna y Flora Silvestres. Iksoo Kim, Illinois State University, very kindly helped by sequencing several specimens for us and Bruce D. Patterson, Field Museum of Natural History, arranged the loan of tissue from FMNH 133049. Thanks to our field colleagues, botanists Luciana Ghermandi and Laura Margutti and mammalogists Nadia Guthmann and Sofía Heinonen Fortabat, and to Jan Decher for preparing the Zusammenfassung.

Zusammenfassung

Analyse der Mitochondrien-DNA und Zoogeographie von zwei Arten von Wüstenseidenmäusen, Eligmodontia, in Patagonien

Wüstenseidenmäuse der Gattung *Eligmodontia* haben den Säugetierkundlern seit langem ein komplexes und etwas ärgerliches taxonomisches Problem bereitet. Zu verschiedenen Zeiten wurden Wüstenseidenmäuse als zu einer oder zu mehreren Arten gehörig betrachtet. In jüngster Zeit haben karyologische Befunde das Vorhandensein von mindestens zwei morphologisch kryptischen Spezies nahegelegt. Um die Hypothese zu prüfen, daß in Patagonien mindestens zwei genetisch unterscheidbare und reproduktiv isolierte Arten leben, haben wir in der vorliegenden Arbeit eine Kombination

aus karyologischen Daten und DNA-Sequenzen des mitochondrialen Cytochrom-b-Gens herangezogen. Mit diesen Methoden konnten wir zeigen, daß *E. morgani* und *E. typus* anhand ihres Karyotyps und ihrer mtDNA leicht voneinander unterschieden werden können. So zeigten sie mehr als 10% Sequenzdivergenz in einem 348bp langen Abschnitt des Cytochrom-b-Gens. Innerhalb jeder Art konnten zahlreiche maternale Linien identifiziert werden. Die Ergebnisse von PAUP-Analysen, die hinsichtlich des Zusammenhanges der Linien mit der geographischen Verbreitung der untersuchten Tiere angestellt wurden zeigten, daß bei jeder Art die älteste Linie selten und auf den nordwestlichen Teil des Untersuchungsgebietes beschränkt war. Jede Art war auch durch eine häufige, geographisch weitverbreitete „Hauptlinie" gekennzeichnet. An jedem Sammelort wurde typischerweise die Hauptlinie, nebst einer oder mehrerer nahe verwandter lokaler Linien gefunden. Diese Daten stimmen mit der Annahme eines historischen genetischen Engpasses, der raschen Ausbreitung der überlebenden Hauptlinie und der anschließenden Weiterverbreitung unter Herausbildung lokaler Linien überein. Die eindeutige Identifikation von Individuen auf der Basis mitochondrialer DNA, die bisher mittels ausschließlich morphologischer Daten nicht möglich war, erlaubte uns den Beginn der Kartierung der Verbreitung der beiden weitgehend allopatrischen Arten. Nach diesen Daten kommt *E. morgani* in eher gemäßigten Habitaten, *E. typus* in eher ariden Gebieten, östlich des Verbreitungsgebietes von *E. morgani*, vor.

References

Allen, J. A. (1901): New South American Muridae and a new Metachirus. Bull. Amer. Mus. Nat. Hist. **14**, 405–412.

Avise, J. C. (1987): Intraspecific phylogeography: the mitochondrial DNA bridge between population genetics and systematics. Ann. Rev. Ecol. Syst. **18**, 489–522.

Avise, J. C. (1994): Molecular Markers, Natural History and Evolution. New York; Chapman and Hall.

Avise, J. C. (1996): Three fundamental contributions of molecular genetics to avian ecology and evolution. Ibis **138**, 16–25.

Brown, W. M.; George, Jr., M.; Wilson, A. C. (1979): Rapid evolution of animal mitochondrial DNA. Cell **26**, 167–180.

Clapperton, C. (1993): Quaternary geology and geomorphology of South America. Amsterdam; Elsevier.

Crandall, K. A.; Templeton, A. R. (1993): Empirical tests of some predictions from coalescent theory with applications to intraspecific phylogeny reconstruction. Genetics **134**, 959–969.

Hershkovitz, P. (1962): Evolution of Neotropical cricetine rodents (Muridae) with special reference to the phyllotine group. Fieldiana Zool. **46**, 1–524.

Hughes, G. A.; Carr, S. M. (1993): Reciprocal hybridization between white-tailed deer (*Odocoileus virginianus*) and mule deer (*O. hemionus*) in western Canada: evidence from serum albumin and mtDNA sequences. Can. J. Zool. **71**, 524–530.

Iriondo, M. H.; Garcia, N. O. (1993): Climatic variations in the Argentine plains during the last 18,000 years. Paleogeog. Paleoclimatol. Paleoecol. **101**, 209–220.

Irwin, D. M.; Kocher, T. D.; Wilson, A. C. (1991): Evolution of the cytochrome b gene of mammals. J. Mol. Evol. **32**, 128–144.

Kelt, D. A.; Palma, R. E.; Gallardo, M. H.; Cook, J. A. (1991): Chromosomal multiformity in *Eligmodontia* (Muridae, Sigmodontinae), and verification of the status of *E. morgani*. Z. Säugetierkunde **56**, 352–358.

Kocher, T. D.; Thomas, W. K.; Meyer, A.; Edwards, S. V.; Pääbo, S.; Villablanca, F. X.; Wilson, A. C. (1989): Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. Proc. Nat. Acad. Sci. USA **86**, 6196–6200.

Lee, M. R.; Elder, F. F. (1980): Yeast stimulation of bone marrow mitosis for cytogenetic investigation. Cytogen. and Cell Gen. **26**, 36–40.

Lehman, N.; Eisenhawer, A.; Hansen, K.; Mech, L. D.; Peterson, R. O.; Gogan, P. J. P.; Wayne, R. K. (1991): Introgression of coyote mitochondrial DNA into sympatric North American gray wolf populations. Evolution **45**, 104–119.

Mares, M. (1977): Water economy and salt balance in a South American desert rodent *Eligmodontia typus*. Comp. Biochem. Physiol. **56 A**, 325–332.

Markgraf, V. (1993): Paleoenvironments and paleoclimates in Tierra del Fuego and southernmost Patagonia. Paleogeog. Paleoclimatol. Paleoecol. **102**, 53–68.

Martin, A. P.; Naylor, G. J. P.; Palumbi, S. R. (1992): Rates of mitochondrial DNA evolution in sharks are slow compared with mammals. Nature **357**, 153–155.

Musser, G. G.; Carleton, M. D. (1993): Family Muridae. In: Mammal Species of the World: A Taxonomic and Geographic Reference. Ed. by D. E. Wilson and D. M. Reeder. Washington D. C.: Smithsonian Institution Press. Pp. 501–756.

Moritz, C. (1994): Applications of mitochondrial DNA analysis in conservation; a critical review. Molec. Ecol. **3**, 401–411.

Ortells, M. O.; Reig, O. A., Wainberg, R. L.; Hurtado de Catalfo G. E.; Gentile de Fronza, T. M. L. (1989): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae) II. Chromosome multiformity and autosomal polymorphism in *Eligmodontia*. Z. Säugetierkunde **54**, 129–140.

Patton, J. L. (1967): Chromosome studies of certain pocket mice, genus *Perognathus* (Rodentia, Heteromyidae). J. Mammalogy **48**, 27–37.

Phillipi, R. A. (1896): Descripción de los mamíferos traídos del viaje de exploración de Tarapacá por Federico Phillipi. Ann. Mus. Hist. Nat. (Chile), Entr. **13 a**, 1–24.

Phillips, C. J.; Pumo, D. E.; Genoways, H. H.; Ray, P. E.; Briskey, C. A. (1991): Mitochondrial DNA evolution and phylogeography in two Neotropical fruit bats, *Artibeus jamaicensis* and *Artibeus lituratus*. In: Latin American mammalogy, History, Biodiversity, and Conservation. Ed. by M. A. Mares and D. J. Schmidly. Norman, OK: Univ. Oklahoma Press. Pp. 97–123.

Pumo, D. E.; Phillips, C. J.; Barcia, M.; Millan, C. (1992): Three patterns of mitochondrial DNA divergence in the meadow vole, *Microtus pennsylvanicus*. J. Mol. Evol. **34**, 163–174.

Redford, K. H.; Eisenberg, J. F. (1992): Mammals of the Neotropics: the Southern Cone. Vol. 2. London: Univ. Chicago Press.

Saiki, R. K.; Scharf, S.; Falooma, F.; Mullis, K. B.; Horn, G. T.; Erlich, H. A.; Arnheim, N. (1985): Enzymatic amplification of β-globin genomic sequence and restriction site analysis for diagnosis of sickle cell anemia. Science **230**, 1350–1354.

Saiki, R. K.; Gelfand, D. H.; Stoffel, S.; Scharf, S. J.; Higuchi, R.; Horn, G. T.; Mullis, K. B.; Erlich, H. A. (1988): Primer directed enzymatic amplification of DNA with a thermostable DNA polymerase. Science **239**, 487–491.

Schäbitz, F. (1994): Holocene climatic variations in northern Patagonia, Argentina. Paleogeog. Paleoclimatol. Paleoecol. **109**, 287–294.

Sikes, R. S.; Monjeau, J. A.; Birney, E. C.; Phillips, C. J.; Hillyard, J. R. (1997): Morphological versus chromosomal and molecular divergence in two species of *Eligmodontia*. Z. Säugetierkunde (in press).

Smith, M. F.; Patton, J. L. (1991): Variation in mitochondrial cytochrome b sequence in natural populations of South American akodontine rodents. Mol. Biol. Evol. **8**, 85–103.

Swofford, D. L. (1993): PAUP: Phylogenetic Analysis Using Parsimony, vers. 3.1.1. Washington D.C.: Smithsonian Institution.

Thomas, O. (1916): On the grouping of the South American Muridae that have been referred to *Phyllotis*, *Euneomys*, and *Eligmodontia*. Ann. Mag. Nat. Hist. **8**, 139–143.

del Valle, H. F.; Labraga, J. C.; Goergen, J. (1995): Biozonas de la Región, Patagónica. In: Evaluación del estado actual de la desertificación en áreas representativas de la Patagonia: Informe Final Etapa I Proyecto. Ed. by INTA-GTZ: Río Gallegos–Trelew–Puerto Madryn–Bariloche.

Zambelli, A.; Dyzenchauz, F.; Ramos, A.; de Rosa, N.; Wainberg, R.; Wilson, A. C. (1992): Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae). III. New data on the distribution and variability of karyomorphs of the genus *Eligmodontia*. Z. Säugetierkunde **57**, 155–162.

Authors' addresses: Jeanna R. Hillyard and C. J. Phillips, Department of Biological Sciences, Illinois State University, Normal, IL 61790-4120, USA; E. C. Birney and R. S. Sikes, James Ford Bell Museum of Natural History and Department of Ecology, Evolution, and Behavior, University of Minnesota, St. Paul, MN 55108 USA; J. A. Monjeau, Departamento de Ecología, Universidad Nacional del Comahue, CC. 1336, Bariloche, Argentina

Z. Säugetierkunde 62 (1997) 293–302

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

On the population fluctuations and structure of the Wood lemming *Myopus schisticolor*

By O. Eskelinen

Department of Biology, University of Joensuu, Joensuu, Finland

Receipt of Ms. 01. 09. 1995
Acceptance of Ms. 13. 11. 1996

Abstract

A population of the wood lemming *Myopus schisticolor* Lilljeborg has been studied in Heinävesi, Finland, for over a period of 15 years from 1982 to 1996 on animals which died during migration. The fluctuations of the population were regular with three year intervals. Migration took place in all peak years. During migration dead animals were collected and measured. Animal size and the number of offspring was greater in the years of growing population density than in the years with decreasing density. The sex ratio changed from 15% to 29% males in different years but there was no correlation between the proportion of males and the population density.

Introduction

The wood lemming *Myopus schisticolor* Lilljeborg occurs sporadically in the coniferous forests of Fennoscandia and Russia (see e.g. Erkinaro 1972; Heinonen 1985; Fedorov et al. 1994). The population density of the wood lemming fluctuates irregularly (e.g. Kalela 1963). When the population becomes very dense the lemmings begin to migrate, but the migrations are short. The migration may occur in a large area at the same time (Kalela 1963; Uino 1963) or in a small area (Skarén 1963; Alaja 1983; Eskelinen et al. 1983, 1984; Skarén et al. 1984). The wood lemming has an exceptionally large majority of females which is thought to cause the population explosion of the species (e.g. Henttonen 1983); the sex ratio is usually 3:1 (Kalela and Oksala 1966). The reason for this exceptional sex ratio is considered to be the unusual sex determination of the species (Fredga et al. 1977), a mutation in the X chromosome causing about half of the XY animals to be females.

Although there are numerous publications concerned with the migration of the wood lemming, only a few investigations have been devoted to a long-term observation of the same population.

The aim of the present study is to clarify the changes in the abundance, migration and the structure of the wood lemming population in Heinävesi, in southeastern Finland, during the years 1982–96. The population is the same as in the earlier publications concerning the years 1982 and 1983 (Eskelinen et al. 1983, 1984).

Material and methods

The abundance of the wood lemming population has been studied by observing the traces (tunnels, faeces and feeding places) of the animals and in the late summer searching for dead animals especially under bridges and precipices and in canals (see Eskelinen et al. 1983).

The railway bridges have proved to be the most effective "traps" (Fig. 1) because when migrating lemmings coming to the railway are forced to follow it. Not being able to go under or over the rails, they come to bridges and many of them fall down several meters and die. There are also several canals in Heinävesi (Fig. 2); when lemmings follow the shores, many of them fall into the canals and die. Traps have not been used except in 1982 (73 trap nights, see ESKELINEN et al. 1983) because numerous animals die anyway at the above-mentioned places.

Fig. 1. Dead wood lemmings on the roadside under the railway bridge in Koivumäki in autumn 1982.

The most advantageous places for collecting were checked daily or at least every two days during migration in August and September. Animals in good condition were stored in deep freeze for later study. Decomposed animals were only counted and not kept for later study.

The most important sites for collecting in 1982 were the railway bridges near Heinävesi station and Koivumäki. These bridges were subsequently repaired and the lemmings could no longer fall between the sleepers onto the road. However, the station bridge continued to be one of the best places for collecting. Other important places were Sappu and Vääräkoski railway bridges and the canals in Kerma and Vihovuonne. The Vaaluvirta bridge was built in 1987 and was one of the sites for future collecting.

The collected animals were measured, weighed, sex-determined, the length of the testes or the diameter of the uterus were measured, and the birth scars of the uterus were checked. The males were considered to be mature when the length of testes was over 6.5 mm (see SKARÉN 1963) and females when birth scars were evident in uterus.

In statistics t-test have been used.

The methods have been similar all through the study period.

Results

Occurrence, changes in abundance and migration

Surrounded by waters and field, the area of occurrence of the present population of lemmings has been the same every year when the population density has been high (ESKELINEN et al. 1983, 1984; SKARÉN et al. 1984).

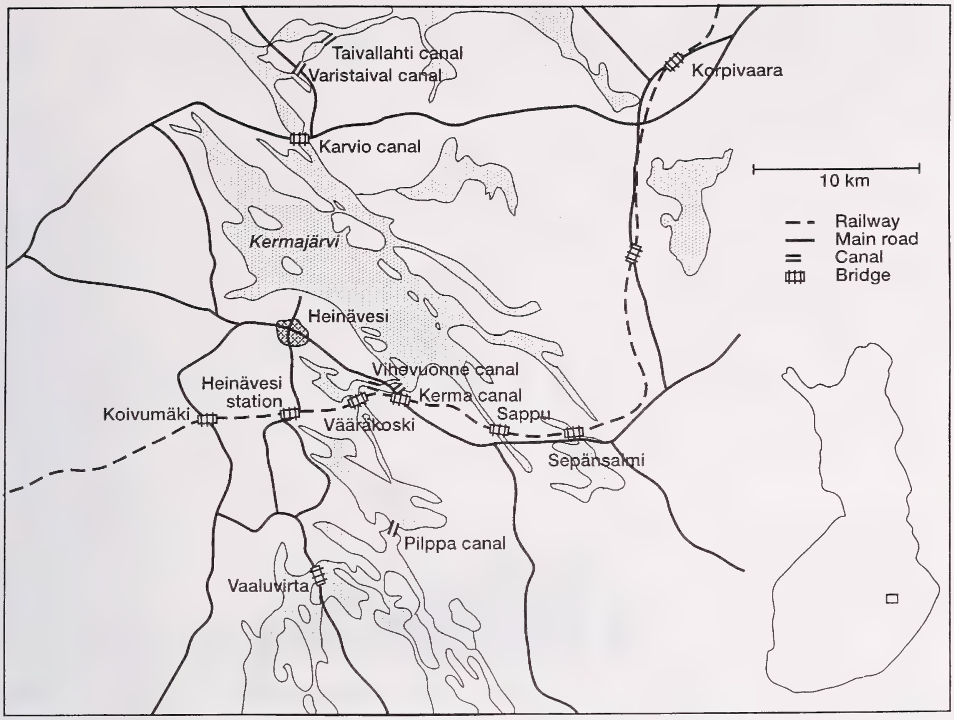


Fig. 2. Map of the study area in Heinävesi showing main waters, roads and collecting sites.

Traces of animals were found in all the observation years except in 1994. When the population density was low only a few traces of animals were found in old spruce forests and swamps where the moss cover is thick. In peak years there were numerous traces in optimal biotopes in summer, in late summer also in pine forests and even in mossy clear-felled areas.

Table 1. The number of wood lemmings found at different sites in different years (rail.br. = railway bridge).

		1982	1983	1986	1989	1992	1995	1996
Vääräkoski	rail.br.	50	28	7	234	121	3	42
Station	rail.br.	350	2	8	224	176	1	29
Vihovuonne	canal	100	5	6	211	67	4	1
Kerma	canal	100		2	138	66		12
Sappu	rail.br.	25	17	15	399	159	18	62
Sepänsalmi	rail.br.	10	2		62	13	12	44
Koivumäki	rail.br.	220	27		20	48		15
Vaaluvirta	road br.				54	17		3
Karvio	canal	20		1	23	9		4
Varistaival	canal	10		2	17	9		4
Taivallahti	canal	10		1	14	9		
Pilppa	canal				28	35		2
Korpivaara	rail.br.	3	46		8	33		
Others		100	61	6	61	80		7
Totals		998	188	48	1 493	842	38	225
Analysed		183	57	27	918	448	25	130

The population density was high in the years 1982, 1983, 1986, 1989, 1992, 1995 and 1996 (Tab. 1). In all these years migrations occured, and lemmings were found far from their usual biotopes. In the interval years dead animals were not found and only a few traces of animals were observed.

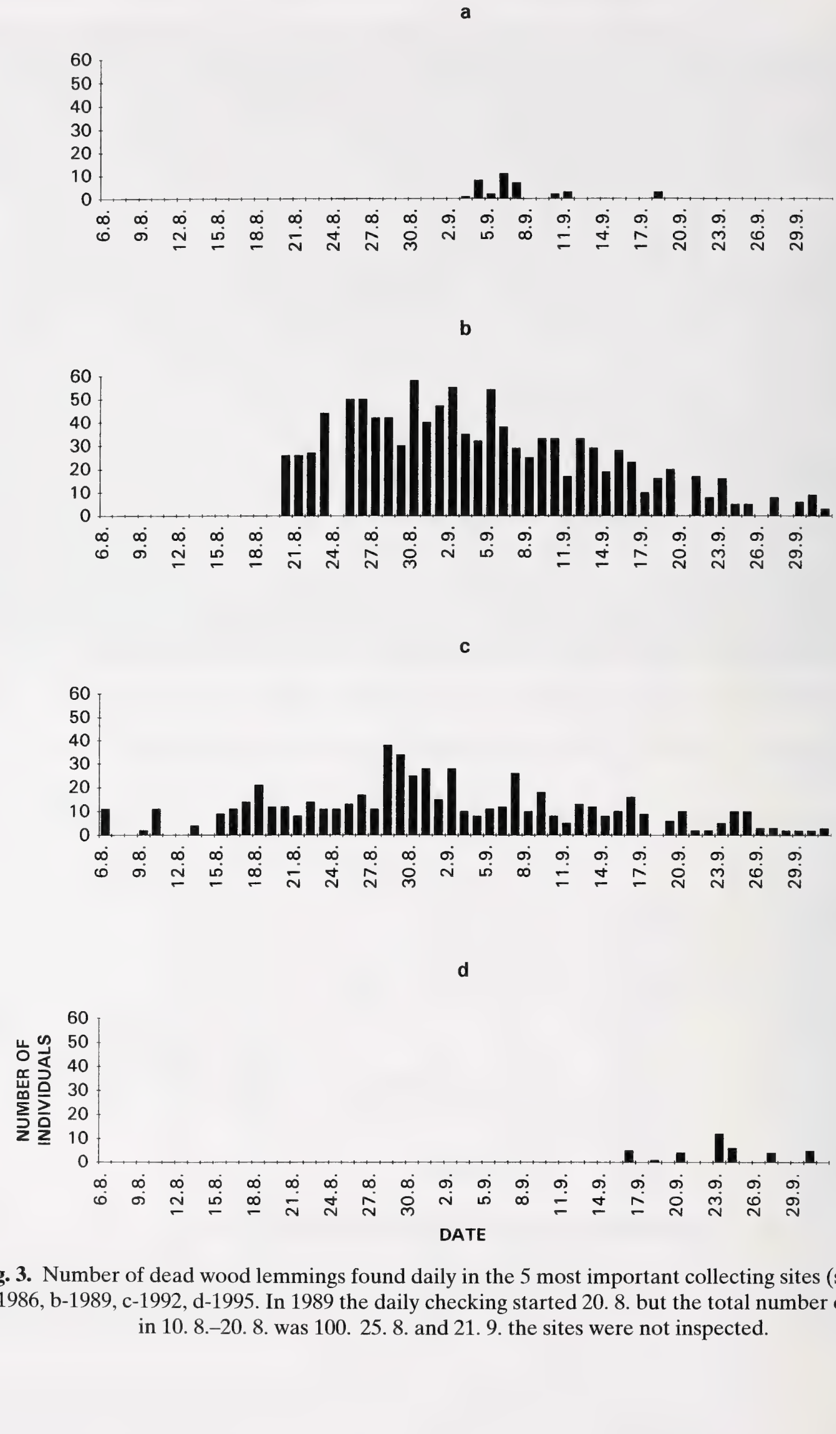


Fig. 3. Number of dead wood lemmings found daily in the 5 most important collecting sites (see Tab. 1) a-1986, b-1989, c-1992, d-1995. In 1989 the daily checking started 20. 8. but the total number of animals in 10. 8.–20. 8. was 100. 25. 8. and 21. 9. the sites were not inspected.

In 1982 (Eskelinen et al. 1983) the migration started at the end of July and ended in the middle of October. About 1 000 dead animals were counted, 183 collected and analysed (Tab. 1).

In 1983 the population density was still high and in late summer migration was again observed (Eskelinen et al. 1984). However, most of the migrating animals were found in different sites than in the previous year and the number of dead animals was small.

The population declined during the winter, began to grow in the summer 1985 and in the following summer numerous traces of animals were found. In the autumn of 1986 migration was again observed. The number of dead animals was, however, small (Fig. 3 a).

In the spring of 1987 traces were found at many cites, in 1988 only a few of them were found, but in 1989 abundant traces were found in snow-free patches after commencement of melting. The wood lemmings had probably bred already during winter or early spring (see e. g. Mysterud 1966). In the late summer the population density was very high, and their migration started at the beginning of August but regular observation was started in the middle of August (Fig. 3 b). Migration was most active at the end of August and in the beginning of September for about two weeks and then gradually slowed down until it ended at the beginning of October. More dead animals were found than ever before, about 1 500, 918 of which were analysed.

The population density appeared to decline in the summer 1990. In 1992 there were numerous traces even in spring and in the late summer the migration began again, and followed the same pattern as in 1989 (Fig. 3 c). Fewer dead animals were found than in 1989, about 800. In the spring of 1993 the population density was still high but decreased in the summer. Only one migrating lemming was found dead in the autumn.

No traces were found in 1994, but in the summer 1995 traces were again observed at many cites and 38 migrating animals were found in the autumn (Fig. 3 d). The migration time was later than in the other years. In the summer 1996 more traces were observed than in the previous year and 225 dead animals were found in August and September.

There was one albino among the small number of dead wood lemmings collected in 1986, and also one in 1992 amongst a large number of 800 animals. In 1989 there were no albinos found amongst 1 500 wood lemmings.

Other animals

There were many short-tailed voles *Microtus agrestis* in the study area in 1982 and 1983 but the dead animals were not counted. From the year 1986 other animal species that were found in the same sites as the wood lemmings were also noted (Tab. 2). The most

Table 2. Number of dead individuals of other small mammal species found at the same sites.

	1986	1989	1992	1995	1996
Short-tailed vole *Microtus agrestis*	22	109	132	27	30
Bank vole *Clethrionomys glareolus*		13	7	5	2
Harvest mouse *Micromys minutus*	1	6	1		
Brown rat *Rattus norvegicus*		1	1		
House mouse *Mus musculus*		1	1		
Common shrew *Sorex araneus*		10	11	8	6
Graves shrew *Sorex isodon*			1	2	1
Pygmy shrew *Sorex minutus*	1			1	
Masked shrew *Sorex caecutiens*					1
Pygmy weasel *Mustela nivalis*					1
Totals	25	142	154	41	41

abundant species is the short-tailed vole. The number of other animals is small. The fluctuation of the short-tailed vole population is similar to that of the wood lemming and a small migration was also found. Quite a large number of dead short-tailed voles were found in the same years as the wood lemmings, but the number of animals was much smaller than that of the wood lemming.

Population structure

There are distinct annual variations in sex ratio, body weight and body length in the population of wood lemmings (Tab. 3). The sex ratio (the proportion of males) was 22% in 1982, 25% in 1983, 15% in 1986, 26% in 1989, 29% in 1992, 16% in 1995 and 21% in 1996, the mean proportion of males being 25%. The low number of males in the small number of animals collected in 1986 and 1995 differs clearly from that of the other years.

Table 3. Body size, sex ratio, sexual maturity and reproduction marks of females (m = male, t = total, f = female, mat = mature, i = immature, scars = scars in uterus).

Sex	Year	N	%	Weight $\bar{X}$ g	SD	Length $\bar{X}$ mm	SD	Testis $\bar{X}$ mm	SD	Scars $\bar{X}$	SD
m t	1982	40	21.8	17.7	1.8	86.0	4.2	3.7	0.5		
	1983	14	24.6	18.3	4.9	86.5	7.2	4.6	2.8		
	1986	4	14.8	15.3	2.0	80.3	3.3	5.1	1.3		
	1989	237	25.8	18.6	2.9	91.0	4.5	3.9	1.2		
	1992	129	28.8	18.5	2.2	89.7	5.6	4.2	1.7		
	1995	4	16.0	18.3	1.2	81.3	4.4	3.3	0.5		
	1996	27	20.8	17.9	3.5	87.3	8.2	3.9	1.6		
m i	1982	40	21.8	17.7	1.8	86.0	4.2	3.7	0.5		
	1983	11	18.3	16.1	2.2			3.3	0.5		
	1986	3	11.1	15.2	2.4	80.3	4.0	3.9	0.8		
	1989	225	24.5	18.2	1.7	91.0	3.6	3.6	0.6		
	1992	117	26.1	18.1	1.4	89.0	5.2	3.7	0.9		
	1995	4	16.0	18.3	1.2	81.3	4.4	3.3	0.5		
	1996	25	19.2	17.1	1.6	85.3	3.7	3.5	0.6		
mmat	1982	0									
	1983	3	5.3	26.3	3.8			9.7	1.2		
	1986	1	3.7	21.1		101		6.6			
	1989	12	1.3	25.4	8.3	101.0	7.4	8.2	1.3		
	1992	12	2.7	22.3	4.2	96.4	5.7	8.7	1.3		
	1995	0									
	1996	2	1.5	27.5	5.5	112.0	9.0	9.0	1.0		
f i	1982	111	60.7	17.4	1.7	84.4	6.2				
	1983	39	68.4	15.5	2.0	79.9	5.0				
	1986	21	77.8	16.6	1.9	80.6	5.2				
	1989	603	65.7	18.1	1.7	90.0	3.5				
	1992	241	53.8	17.7	1.6	87.6	5.1				
	1995	19	76.0	17.7	1.4	82.6	4.3				
	1996	86	66.2	16.0	1.6	84.2	3.9				
fmat	1982	32	17.5	22.9	3.0	94.6	4.7			5.8	2.3
	1983	4	7.0	19.8	3.7	84.0	6.1			2.8	1.0
	1986	2	7.4	22.2	0.2	95.0	1.4			5.0	0.0
	1989	78	8.5	23.3	4.0	99.0	5.6			5.8	2.6
	1992	78	17.4	22.1	3.9	94.0	7.8			4.8	2.0
	1995	2	8.0	25.0	0.0	101.0	1.4			7.0	1.4
	1996	17	13.1	19.1	2.2	89.9	5.6			3.4	1.5

The differences in the mean sex ratio (25) are not, however, statistically significant. The greatest proportion of males in 1992 (29%) differs only slightly ($p = 0.1$) from that of 1982 (22%).

The mean body weight of young females in 1983 was significantly smaller ($p < 0.001$) than in 1982 (Tab. 3). The difference in the body weight of males is not statistically significant. In 1986 the young females were significantly smaller ($p < 0.05$) than in 1982. In 1989 the young females were significantly larger ($p < 0.01$) than in 1982, but the weights of young males do not differ significantly. In 1992 the young females and males were about the same weight as in 1982 but the young females in 1992 were significantly smaller ($p < 0.001$) than in 1989. In 1995 the young females were of the same weight as in 1982 and 1992. In 1996 the young females were significantly smaller ($p < 0.001$) than in the other years except in 1983 and 1986 and also the young males were significantly smaller ($p < 0.001$) than in 1989 and 1992.

The mean body weight of mature females (Tab. 3) was in 1992 significantly lower ($p < 0.05$) than in 1989 and in 1996 it was significantly lower ($p < 0.001$) than in 1982, 1989 and 1992.

The differences in the body length were quite similar to those in weight (Tab. 3). In 1989 young males and young and mature females were significantly bigger ($p < 0.001$) than in 1982 and 1992.

The mean size of testes of mature males was largest in 1992 when the proportion of mature males was also largest. In the material from 1989 the size of testes was slightly smaller. There are no yearly differences in the mean size of the testes of young males.

There is a clear positive correlation between body weight and maturity both in males and females (Tab. 3).

The proportion of mature females that have produced young was the same, 17.5% in the peak years 1982 and 1992, in 1996 13.1% but in the peak year 1989 only 8.5%, in 1995 8% and in 1983 and 1986 still smaller.

The mean number of the scars of the uterus was 5.8 in 1982 ($n = 32$) and 1989 ($n = 78$), but in 1992 it was 4.8 ($n = 78$). Also more females had embryos in 1992 than in the other years (embryos have also been counted as scars of the uterus in Tab. 3). In 1983 and 1996 the number of scars was significantly ($p < 0.001$) smaller than in the other years.

Discussion

Changes in the abundance and migration in different areas

Unlike other voles, the population fluctuations in the wood lemming are known to be irregular (e. g. Kalela 1963). There are no observations of wood lemmings in many areas between the years of population explosion. In the population at Heinävesi the change in abundance, however, forms a regular cycle with three-year intervals at least during the study period. Moreover, the peak occurrences coincides with that of the short-tailed vole. There are also many observations in the interval years. Also in Kuhmo (Skarén 1972) the change in abundance has been regular with 4–5 year intervals.

The population explosion and related migration of the wood lemming may happen in different areas at the same time as in 1982 (Savolainen et al. 1982; Skarén et al. 1984) or only locally in a small area. In 1989 migration was also observed, for instance, in Rautjärvi, 100 km southeast of Heinävesi (S. Pasanen unpubl.). In Kontiolahti, 100 km northeast of Heinävesi, there was a migration in 1991 (T. Tast unpubl.), when the population density was low in Heinävesi, but there was a population explosion in the following year, as well as in Ilomantsi, 50 km NE of Kontiolahti (H. Hyvärinen unpubl.). The interval of the two large population explosions and migrations (1989 and 1992) in Heinävesi was only three years, which might be unusual.

Population density mostly declines after migration and is very low thereafter (e. g. Kalela 1963). The population density in Heinävesi has often been high over the winter following a migration but has declined during the following spring or summer. In 1983 the population density was, however, high after migration and a small migration was observed in the year thereafter (Eskelinen et al. 1984). The population peak had moved a little to the east of the main area of the previous year. In 1995 a small migration was observed in the growing phase of the population density and a larger migration in the following year while the population was declining. In the district of Rovaniemi Uino (1963) has also observed migrations in two successive years (1957 and 1958).

The course of the migration was much the same in all the years. It started in the first half of August, being most active at the end of August or at the beginning of September and ceased at the end of September or the beginning of October. In 1995, however, the migration time occurred in late September, but the number of animals was small. Elsewhere, e. g. in Rovaniemi (Uino 1963), the time of the migration has been similar.

Comparison of population structure

The mean body weight and length of young males and females does not differ from corresponding material in south Norway (Kratochvil et al. 1979). Judging from the literature (Ilmén and Lahti 1968; Kratochvil et al. 1979), the largest males (46 g) and females (32 g) are born in the previous autumn, the others in the same year. The mean weight of mature females is 4–6 g greater than that of immature ones, but there is a great difference between individuals, while the lightest mature (produced young) female weighed only 15.5 g. According to Skarén (1963) a female is able to breed when its weight reaches 15 g.

The largest males whose testes measured 9–11 mm are born early in the spring or in the previous autumn. The medium-sized animals whose testes are 6.5–8 mm have apparently just become mature or are close to reaching maturity. The small male lemmings are young and immature.

There were no mature males in my material from 1982, the same being true in the material of Skarén et al. (1984) collected partly from the same area at the same time in Heinävesi and Vesanto. However, there were three mature males in the small material from 1983 and one in 1986. In 1992 the proportion of mature males was larger than in the previous peak year 1989, but the difference is not statistically significant.

There are only very few old males in my large collection, similar to the material collected in Rovaniemi in 1957 (Kalela 1963). According to Skarén et al. (1984) the old males obviously die before autumn. Less than 4% of the migrating females were born before summer in the material of Skarén et al. (1984).

The positive correlation between body weight and maturity is similar to that found by Ilmén and Lahti (1986) among female wood lemmings and by Heikura and Lindgren (1977) among male short-tailed voles.

Breeding effectiveness becomes evident from the number of young animals per female that has been greater in the years of growing population density than in the phase of decreasing density. The mean litter size was slightly larger (5.2) in the peak years than according to Kalela and Oksala (1966) in northern Finland (4.5). According to Skarén (1963) the females born in the previous year have 4.6 and the females born in the same year 3.5 young, on average.

The size of animals appears to be related to their breeding effectiveness because the size of the lemmings was larger in the growing than in the decreasing population. In 1982, 1989, 1992, and 1995 while the population was growing in the autumn the size of the lemmings was greater than while the population was decreasing in 1983 and 1996. According to Hyvärinen (1984) the size of animals affects their ability to take care of their young.

Sex ratio

It appears that the purpose of the female majority especially in the growing phase of the population is to produce a great number of offspring quickly (Henttonen 1983). The sex ratio has changed greatly in different years but the mean proportion of males does not differ from the expected value of 25% males. According to many studies (Skarén 1963; Kalela and Oksala 1966; Frank 1966; Gileva and Fedorov 1990) the sex ratio changes greatly in the course of a year and the proportion of males is usually smaller in the autumn than in the summer.

Reasons for the fluctuations and migrations of the population

Some observations confirm the known opinions concerning the reasons for fluctuation and migration of population. Some refer to the role of disease in taxing the population. In the late summer 1983 many wood lemmings were seen moving slowly in the daytime and obviously ill. The animals that were caught alive usually died within a few days. Listeriosis was found to be the cause of death for the wood lemmings caught alive by Skarén (1981).

Over 90% of the food of the wood lemming is moss (Andreassen and Bondrup-Nielsen 1991 a), the sufficiency of which in the wintering areas is important for the lemming to be able to breed during the winter (Mysterud et al. 1972). The scarcity of moss is supported by field observations especially from 1983 when the population density was high during two successive years. Skarén's (1971) observations also agree with this.

The main reason for regular migration in an area divided by waters like Heinävesi is obviously the scarcity of living space. Although the home ranges of wood lemmings are small (Andreassen and Bondrup-Nielsen 1991 b), the living space may still become overcrowded when the population density is high. Animals were clearly observed to settle down in new areas and breed there in 1983 (Eskelinen et al. 1984). Another reason for a migration is thought to be lemmings search for new wintering areas. According to many observations, popular wintering areas were mossy northern slopes even in pine forests where the lemmings were not observed in the summer before migration.

Acknowledgements

I am grateful to Prof. Heikki Hyvärinen who gave me valuable advice on writing this study, to Timo Hokkanen who participated in the handling of the material, to Seppo Kotilainen who helped in computer processing and to many others who helped in collecting the material. Mr. Edward Abraham checked the English manuscript.

Zusammenfassung

Über Populationsfluktuationen und -struktur des Waldlemmings Myopus schisticolor

Die Population des Waldlemmings ist in der Region von Heinävesi seit 15 Jahren untersucht worden. Fluktuationen der Populationsdichte erfolgten regelmässig in Perioden von drei Jahren. In allen Spitzenjahren wurden Wanderungen festgestellt. Bei Wanderungen verunglückte Tiere konnten gesammelt und gemessen werden. Die Grösse der Tiere und die Anzahl der Jungen war in den Jahren mit wachsender Populationsdichte grösser als in den Jahren, als die Populationsdichte sich verminderte. Das Verhältnis der Geschlechter wechselte von 15% bis 29% Männchen in verschiedenen Jahren, aber es gibt keine Korrelation zwischen dem Anteil der Männchen und der Populationsdichte.

References

Alaja, P. (1983): Havaintoja metsäsopulista, *Myopus schisticolor*, ja muista pikkunisäkkäistä, Micromammalia, Vesannolla 1979–1982. Lounais-Hämeen Luonto **69**, 5–12.

Andreassen, H. P.; Bondrup-Nielsen, S. (1991 a): A comparison of the effects of a moss diet and a varied diet on the growth of juvenile wood lemmings, *Myopus schisticolor* (Lilljeb.). Z. Säugetierkunde **56**, 378–379.

– 1991 b): Home range size and activity of the wood lemming, *Myopus schisticolor.* Holarctic Ecol. **14**, 138–141.

Erkinaro, E. (1972): Skoglämmelns, *Myopus scisticolor*, utbredning i Skandinavien. Fauna Flora **67**, 30–42.

Eskelinen, O.; Hokkanen, T.; Kuhlman, E.; Markkula, I. (1983): Migration of the wood lemming, *Myopus schisticolor* Lilljeb., in 1982 at Heinävesi, southeastern Finland. Luonnon Tutkija **87**, 144–146.

Eskelinen, O.; Hokkanen, T. J.; Kuhlman, E. (1984): The spreading and changes in abundance of the wood lemming, *Myopus schisticolor* Lilljeb., at Heinävesi, southeastern Finland. Luonnon Tutkija **88**, 167–169.

Fedorov, V. B.; Frederiksson, R.; Fredga, K. (1995): Genetic differentiation among populations of the wood lemming, *Myopus schisticolor* – isozyme variation. Heredity **74**, 267–273.

Frank, F. (1966): Verschiebung des Geschlechtsverhältnisses in der Wühlmaus-Gruppe (Microtidae). Naturwiss. **53**, 90.

Fredga, K.; Gropp, A.; Winking, H.; Frank, F. (1977): A hypothesis explaining the exceptional sex ratio in the wood lemming (*Myopus schisticolor*). Hereditas **85**, 101–104.

Gileva, E. A.; Fedorov, V. B. (1991): Sex ratio, XY females and absence of inbreeding in a population of the Wood Lemming, *Myopus schisticolor* Lilljeborg, 1844. Heredity **66**, 351–355.

Heikura, K.; Lindgren, E. (1977): Reproduction in the field vole, *Microtus agrestis* L., in the vicinity of Oulu, Finland. Aquilo Ser Zool. **19**, 33–43.

Heinonen, R. (1985): Metsäsopulin (*Myopus schisticolor)* levinneisyydestä ja esiintymisrytmiikasta Suomessa. Luonnon Tutkija **89**, 164–169.

Henttonen, H. (1983): Metsäsopulin sukupuolen määräytyminen. In: Suomen eläimet 1. Ed. by I. Koivisto, Espoo, Weilin and Göös. P. 127.

Hyvärinen, H. (1984): Wintering strategy of the voles and shrews in Finland. Spec. Publ. Carnegie Museum Nat. Hist. Pp. 139–148.

Ilmén, M.; Lahti, S. (1968): Reproduction, growth and behaviour in the captive wood lemming, *Myopus schisticolor* (Lilljeb.). Ann. Zool. Fenn. **5**, 207–219.

Kalela, O. (1963): Die geographische Verbreitung des Waldlemmings und seine Massenvorkommen in Finnland. Arch. Soc. “Vanamo” **18**, 47–55.

Kalela, O.; Oksala, O. (1966): Sex ratio in the wood lemming *Myopus schisticolor* (Lilljeb.), in nature and in captivity. Ann. Univ. Turkuensis **37**, 5–24.

Kratochvil, J.; Barus, V.; Tenora, F.; Wiger, R. (1979): Contribution to our knowledge of the wood lemming, *Myopus schisticolor.* Folia Zool. **28**, 193–207.

Mysterud, I. (1966): Fortplantning hos skoglemen (*Myopus schisticolor* Lilljeb.) i vinterhalvået. Fauna **19**, 79–83.

Mysterud, I.; Viitala, J.; Lahti, S. (1972): On winter breeding of the wood lemming. Norwegian J. Zool. **20**, 91–92.

Savolainen, E.; Kauppinen, J.; Skarén, U. (1982): Sopulit, salaperäiset vaeltajat. Kuopion museo, luonnontieteellisiä näyttelyjulkaisuja **2**, 1–30.

Skarén, U. (1963): Zur Fortplanzungsbiologie des Waldlemmings. Arch. Soc. “Vanamo” **18** (suppl.), 2–28.

– (1971): Eräs pohjoissavolainen pikkunisäkäskannan huippu ja sen romahdus. Savon Luonto **3**, 1–10.

– (1972): Fluctuations in small mammal populations in mossy forests of Kuhmo, eastern Finland, during eleven years. Ann. Zool. Fenn. **9**, 147–151.

– (1981): Listeriosis killing wood lemmings, *Myopus schisticolor* Lilljeb. Z. Säugetierkunde **46**, 395–396.

Skarén, U.; Savolainen, E.; Jäderholm, K.; Kauppinen, J. (1984): On the occurrence and migration of the wood lemming (*Myopus schisticolor*) in Savo in 1963–83. Kuopion Luonnontieteellisen Museon sarja **6**, 5–22.

Uino, K. (1963): Die Wanderungen des Waldlemmings in Finnland in den Jahren 1956–1958. Arch. Soc. “Vanamo” **18** (suppl.), 67–80.

Author's address: Olavi Eskelinen, Department of Biology, University of Joensuu, Box 111, FIN-80101 Joensuu, Finland

Z. Säugetierkunde **62** (1997) 303–311

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Biochemical systematics of the Wood mouse, *Sylvaemus sylvaticus* (L., 1758) sensu lato (Rodentia, Muridae) from eastern Europe and Asia

By S. V. Mezhzherin

Schmalhausen Institute of Zoology, National Academy of Sciences of Ukraine, Kiev, Ukraine

Receipt of Ms. 01. 02. 1995
Acceptance of Ms. 15. 12. 1996

Abstract

A reexamination of species identity of oriental subspecies of *Sylvaemus sylvaticus* are performed on the basis of allozyme data. Practically all oriental *S. sylvaticus* subspecies (*charkovensis*, *baessleri*, *mosquensis*, *ciscaucasicus*, *uralensis*, *tsherga*, *pallipes*) have been identified as *S. microps s. l.* Only *S. s. vohlynensis* is identical to nominative *S. sylvaticus*. The most eastern forms of wood mouse, *kastschenkoi*, from the Altai mountains, and, *pallipes*, from Tadjikistan, can be characterized by fixed allelic variants at a few loci distinguishable both from nominative *S. microps* and one another at the allospecies level. Taxonomic analysis confirms that the name *uralensis* Pallas, 1811, is the oldest available name for a group of *S. microps*-like forms.

Introduction

Despite large interest in the wood mice genus *Sylvaemus* Ognev, 1924, the systematic problems of this taxonomic group have not solved. This may be due to both wide geographic and individual variability throughout the area and by chromosome formula stability. Only in the last decade after implication of biochemical genetic data, has the wood mice genus *Apodemus s. l.* been revised. The main results were: (i) the genera distinctness of eastern (*Apodemus* and *Alsomys*) and western (*Sylvaemus* and *Karstomys*) Palearctic subgenera (Gemmeke 1980; Iskandar and Bonhomme 1984; Britton-Davidian et al. 1991; Mezhzherin and Zykov 1991; Filippucci 1993); (ii) species level differentiation of the following taxa: *S. alpicola* (Heinrich, 1952) (Storch and Lütt 1989; Vogel et al. 1992), *S. fulvipectus* Ognev, 1924 (= *falzfeini* Mezhzherin and Zagorodnyuk, 1989) (Mezhzherin and Zagorodnyuk 1989; Vorontzov et al. 1992), *S. hermonensis* (Filippucci, Simson et Nevo, 1989) (Filippucci et al. 1989), *S. hyrkanicus* (Vorontzov, Boeskorov, Mezhzherin, 1992) (Vorontzov et al. 1992), *S. ponticus* (Sviridenko, 1936) (Mezhzherin 1991; Vorontzov et al. 1992).

The wood mouse *S. sylvaticus* (L., 1758) is one of the widest geographically distributed species of Palearctic muroid rodents. Its range extends from central Asian mountains and the Altai on the east, to northern Africa and the British Isles on the west. Biochemical variation analysis of *Sylvaemus sylvaticus* s. lato populations of eastern Europe and Asia have detected that several subspecies of *S. sylvaticus* (*S. s. uralensis*, *S. s. charkovensis*, *S. s. tsherga*, *S. s. mosquensis* and *S. s. ciscaucasicus*) were found to be geographic forms of *S. microps* (Mezhzherin 1987, 1990; Mezhzherin and Zykov 1991; Mezhzherin and Mikhailenko 1991; Mezhzherin et al. 1992; Vorontzov et al. 1992).

Nevertheless, these results require generalization. Therefore, the main task of the investigation consisted in summarizing of biochemical variation and differentiation data of wood mice, *S. sylvaticus*, geographic forms from the former USSR territory.

Material and methods

Electrophoretic analysis was carried out on 293 specimens representing populations of *S. s. sylvaticus* live-trapped throughout the former USSR territory in Armenia, Belorussia, Russia, Ukraine, and Tadjikistan. A list of investigated subspecies, their collecting sites, and the number of specimens examined for each taxon are presented in table 1. Sample localities are illustrated in figure 1.
Each specimen was tested in the laboratory for plasma and hemolysed red cells, and tissue samples (liver, kidney, muscle) were immediately studied by standard vertical 7.5% acrylamide gel electrophoresis. Muscle, kidney and liver were homogenized in distilled water containing 5% sucrose and tested for the enzymes and proteins listed in table 2.

Loci were designated according to nomenclature adapted for laboratory mice strains (Bonhomme et al 1984). Allozymes were designated numerically according to their mobility, relative to the most common allele (= 100) in *S. s. sylvaticus* specimens (< 100 = slower mobility; > = faster mobility). In present study included loci of nonspecific esterases having a reliable homology in *S. microps* and *S. sylvaticus* by electrophoretic interspecies comparison.

The genetic divergence between taxa was estimated with the indices of standard (Nei 1975) and unbiased (Nei 1978) genetic distances. A dendrogram of genetic relationship among populations was obtained by using an UPGMA algorithm.

Table 1. Number of specimens examined by electrophoretic procedures for each subspecies and locality

N	Taxa	Localities		n
1	*S. s. sylvaticus*	Slovakia	Komarno	3
		Ukraine	Cherkassy region	7
			Nikolaev region	26
			Odessa region	5
		Moldova	Kishinev	8
2	*S. s. vohlynensis*	Ukraine	Kiev region	23
		Belorussia	Gomel region	14
3	*S. s. charkovensis*	Ukraine	Charkov region	6
			Lugansk region	12
			Cherson region	30
4	*S. s. baessleri*	Ukraine	Crimea	6
5	*S. s. mosquensis*	Russia	Moskow region	12
6	*S. s. ciscaucasicus*	Russia	Kabardino-Balkaria	14
			Northern Osetia	7
			Krasnodar region	4
		Armenija	Khosrov reserve	5
7	*S. s. uralensis*	Russia	Saratov region	2
			Uralsk region	8
			Kurgan region	6
			Chelabinsk region	3
8	*S. s. kastschenkoi*	Russia	Altai	37
9	*S. s. pallipes*	Tadjikistan	Komsomolabad district	9
10	*S. microps*	Slovakia	Komarno	5
		Moldova	Kishinev region	36
		Ukraine	Nikolaev region	4

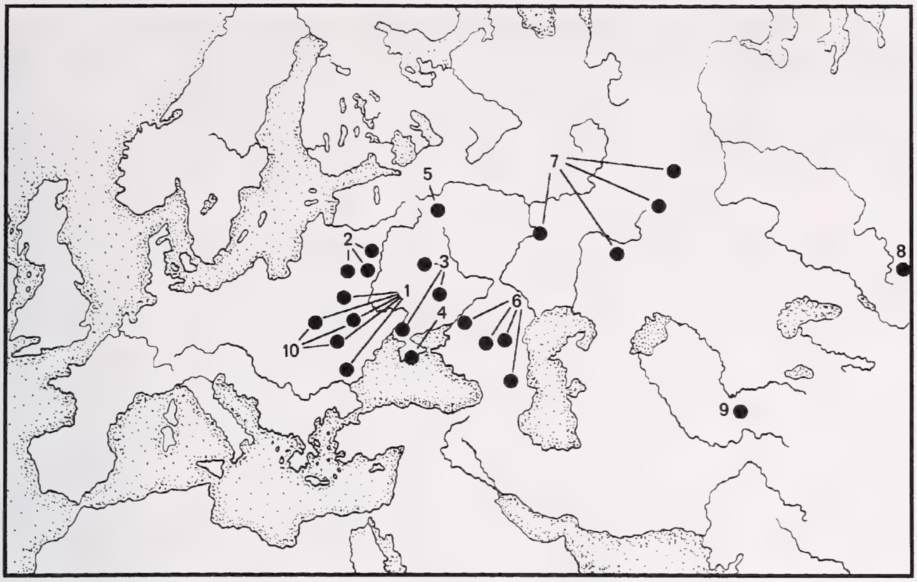


Fig. 1. Sample localisations of *S. sylvaticus* taxa and *S. microps* populations used in genetic investigations.

Table 2. Buffer systems, loci scored and tissue expression in the analysis of *S. sylvaticus* s. l.

Enzyme or protein	E.C. number	Locus	Tissue	Buffer system
Albumin		Alb	l, m, pl	B
Alcohol dehydrogenase	1.1.1.1	Adh-1	l	A
Aspartate aminotransferase	2.6.1.1	Aat-1, 2	m, k, l	A
Carbone anhydrase	4.2.1.1	Car-1	hem	A, B
Creatine kinase	2.7.3.2	Ck-2	m	A, B
Diaphorase	1.6.2.2	Dia-1, 2	h	A, B
Esterase	3.1.1.1	Es-1, 2, a	pl	B
		Es-9, 15	m	A, B
		Es-3, 6, 10	k	A, B
Glucose-6-phosphate dehydrogenase	1.1.1.49	Gpd-x	k, l	A
Glycerol-3-phosphate dehydrogenase	1.1.1.8	Gdc-1	k, m	A
Hemoglobin		Hb-A, B	hem	A, B
Isocitrate dehydrogenase	1.1.1.42	Idh-1	l, k	A
		Idh-2	m	A
Lactate dehydrogenase	1.1.1.27	Ldh-A	m, k, l	A
		Ldh-B	k, m	A
Malate dehydrogenase	1.1.1.37	Mor-1, 2	m, k, l	A
Malic enzyme	1.1.1.40	Mod-1, 2	m, k, l	A
Phosphoglucomutase	2.7.5.1	Pgm-1	m	B
		Pgm-2	m, k, l	B
Phosphogluconate dehydrogenase	1.1.1.44	Pgd	m, k, l	A
Postalbumin		Post	pl	B
Superoxide dismutase	1.15.1.1	Sod-1	m, l	A
		Sod-2	m	B
Sorbitol dehydrogenase	1.1.1.14	Sdh	l, k	A
Transferrin		Tf	p	B
Xanthine dehydrogenase	1.2.3.2	Xdh	l	A

Buffer type abbreviations are as follows: A – continuous Tris-EDTA-borate (pH 8.5) (Peacock et al. 1965), B – discontinuous Tris-glycine (pH 8.3) and Tris-HCl (pH 8.7) (Davis 1964). k – kidney, l – liver, m – muscle, hem – hemolysate, pl – plasma.

Table 3. Allelic frequencies at variable loci of *S. sylvaticus* s. l. subspecies

Loci	Alleles	1 *S. s. sylv.*	2 *S. s. vohl.*	3 *S. s. char.*	4 *S. s. baes.*	5 *S. s. mos.*	6 *S. s. cis.*	7 *S. s. ural.*	8 *S. s. tscher.*	9 *S. s. pall.*	10 *S. micr.*
Aat-2	–100	1.00	1.00	1.00	1.00	1.00	0.95	1.00	1.00	1.00	1.00
	–105						0.05				
Car-1	100	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00
	111						0.10				
Es-1	90			0.10	0.10						0.50
	93									0.89	
	95			0.90	0.80	1.00	1.00	1.00	1.00		0.50
	96									0.11	
	98	0.20			0.10						
	100	0.80	1.00								
Es-2	98							0.15			
	99									0.89	
	100			1.00	1.00	1.00	0.95	0.80	1.00		1.00
	102									0.11	
	105						0.05				
	110	1.00	1.00					0.05			
Es-3	100	1.00	1.00								
	110			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Es-9	100	1.00	1.00	1.00	1.00	1.00	1.00	0.66	1.00	1.00	1.00
	102							0.34			
Es-10	99	1.00	1.00								
	100			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Es-15	99						0.05				
	100	1.00	1.00	1.00	1.00	1.00	0.95	0.72	1.00	1.00	1.00
	101							0.28			
Es-a	100	1.00	1.00								
	100[f]			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Gdc-1	95	0.09	0.18						0.13		
	100	0.64	0.70	0.25	0.80	0.23	0.15	0.07	0.87	0.81	0.50
	102									0.19	
	105	0.27	0.12	0.75	0.20	0.77	0.85	0.93			0.50
Hb-B	100	1.00	1.00								
	115			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Idh-1	95	0.22	0.47	0.98	1.00	1.00	1.00	1.00	1.00		1.00
	95.5									1.00	
	98	0.78	0.53								
	100			0.02							
Idh-2	98						0.02				
	100	1.00	1.00	1.00	1.00	1.00	0.98	1.00	1.00	1.00	1.00
Ldh-A	–100			0.02							
	100	1.00	1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00	1.00
Ldh-B	98	1.00	1.00								
	100			1.00	0.98	1.00	1.00	1.00	1.00	1.00	1.00
	102				0.02						
Mod-1	100			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	105	1.00	1.00								

Table 3. (Continued)

Loci	Alleles	1 *S. s. sylv.*	2 *S. s. vohl.*	3 *S. s. char.*	4 *S. s. baes.*	5 *S. s. mos.*	6 *S. s. cis.*	7 *S. s. ural.*	8 *S. s. tscher.*	9 *S. s. pall.*	10 *S. micr.*
Pgd	100	1.00	1.00	0.96	0.50	0.76	0.73	0.75	1.00	1.00	1.00
	104			0.04	0.50						
	105					0.24	0.27	0.25			
Post	100	1.00	1.00	1.00	1.00	1.00	0.90	1.00	1.00	1.00	1.00
	110						0.10				
Sod-1	100			1.00	1.00	1.00	1.00	1.00	1.00	1.00	1.00
	110	1.00	1.00								
Tf	90	0.88	0.84								
	92			0.02		0.07		0.07			
	95	0.07	0.16								
	97.5									0.61	
	98			0.28	0.60	0.32	0.50	0.49	1.00		0.65
	99.5									0.39	
	100			0.65	0.40	0.50	0.46	0.42			0.31
	101	0.05									
	102			0.05		0.11	0.04				0.04
	105							0.02			
Xdh	97			0.17		0.08	0.15		0.37		0.07
	100	0.81	0.75	0.83	1.00	0.92	0.85	1.00	0.63	1.00	0.93
	102	0.19	0.25								
n		59	37	48	6	12	30	19	37	9	45
H obs, %		4.56	4.08	4.08	4.66	4.11	6.00	6.19	1.83	3.77	4.42
H exp, %		4.89	5.33	4.17	4.67	4.14	6.25	7.19	1.86	3.78	4.17
A		1.19	1.14	1.25	1.14	1.17	1.25	1.28	1.06	1.14	1.14
P, 1%		13.9	11.1	19.4	13.9	11.1	30.5	19.4	5.6	13.9	11.1

1 – *S. s. sylvaticus*, 2 – *S. s. vohlynensis*, 3 – *S. s. charkovensis*, 4 – *S. s. baessleri*, 5 – *S. s. mosquensis*, 6 – *S. s. ciscaucasicus*, 7 – *S. s. uralensis*, 8 – *S. s. kastschenkoi*, 9 – *S. s. pallipes*, 10 – *S. microps*.

Results

Biochemical variation.

Sixteen out of 36 loci analysed were monomorphic and fixed for the same allele in all populations studied; Adh-1, Aat-1, Ck-2, Dia-1,2, Es-6, Gpd-X, Mor-1,2, Mod-2, Pgm-1,2, Sdh, Sod-2, Hb-A, Alb. The allele frequencies of variable loci in the taxa analysed are given in table 3.

Levels of genetic variation are given in table 3: mean number of alleles per locus (A); mean proportion of heterozygosity observed (Hobs) and expected (Hexp); proportion of polymorphic loci per population (P, I%).

A high level of polymorphism was found at the following loci: Gdc-1, Idh-1, Tf, Es-1,2, Pgdh, Xdh, in at least one subspecies or population. Eight loci: Aat-2, Car-1, Es-9,15, Idh-2, Ldh-A,B, Post had only rare allelic variants. Average estimation of intrapopulation genetic variation (Tab. 3) was higher than usually observed in mammals (Nevo et al. 1984; Mezhzherin 1992); range was from H obs = 0.018 to 0.062 with mean H obs = 0.044. The highest levels H obs = 0.06 and 0.062 were found in *S. s. uralensis* and *S. s. ciscaucasicus*, respectively, whereas the lowest ones were revealed in Altay subspecies H obs = 0.018.

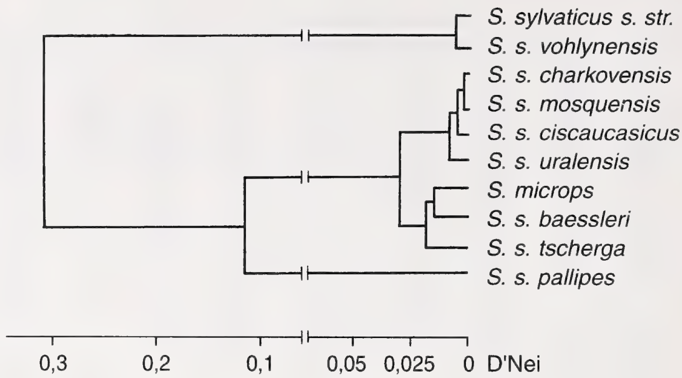


Fig. 2. UPGMA phenogram of genetic distances (Nei 1975) between *S. sylvaticus* taxa and *S. microps* based on 36 biochemical loci.

Table 4. Matrix of standard Nei's (1975) genetic distances (below diagonal) and unbiased Nei's (1978) genetic distance (above diagonal) among *S. sylvaticus* s. l. subspecies

Taxa	N	1	2	3	4	5	6	7	8	9	10
S. sylvaticus s. str	1	0	0.003	0.251	0.252	0.258	0.254	0.257	0.258	0.248	0.244
S. s. vohlynensis	2	0.004	0	0.250	0.244	0.268	0.269	0.262	0.248	0.258	0.238
S. s. charkovensis	3	0.312	0.309	0	0.018	0.001	0.004	0.011	0.028	0.092	0.011
S. s. baessleri	4	0.312	0.307	0.019	0	0.010	0.018	0.017	0.011	0.093	0.012
S. s. mosquensis	5	0.316	0.313	0.002	0.017	0	0.001	0.011	0.038	0.100	0.011
S. s. ciscaucasicus	6	0.324	0.323	0.005	0.021	0.002	0	0.023	0.031	0.111	0.012
S. s. uralensis	7	0.327	0.327	0.012	0.029	0.008	0.008	0	0.041	0.112	0.023
S. s. kastschenkoi	8	0.319	0.309	0.029	0.017	0.029	0.029	0.041	0	0.101	0.022

Genetic differentiation

Eleven loci displayed fixation of alternative alleles (Idh-1, Ldh-B, Mod-1, Sod-1, Es-1, Es-2, Es-3, Es-10, Es-a, Hb-B, Tf) among part of the populations. From the allele frequencies at 36 loci studied, Nei's genetic distance (D) was calculated between taxa (Tab. 4). An UPGMA dendrogram summarizing the genetic relationships between the taxa investigated is given in figure 2.

There are two main clusters present in the phenogram. One of them consists of the nominative *S. s. sylvaticus* and includes *S. s. vohlynensis* also, the second cluster combines *S. microps* with all other taxa. The mean of standard Nei's genetic distance (Nei 1975) between "*sylvaticus*"-like and "*microps*"-like taxa is D = 0.313, which corresponds to a level of interspecies differentiation. The genetic distance between *S. s. vohlynensis* – *S. s. sylvaticus* was very low (D = 0.004). The mean genetic distance among "*microps*"-like group was higher, D = 0.041 ranging from 0.002 to 0.124. A valuable level of genetic differentiation among "*microps*"-like taxa appeared with the *S. s. pallipes.* Its mean genetic distance from the other "*microps*"-like taxa was D = 0.113, which corresponds to genetic differentiation of allopatric species.

The levels of genetic differentiation supported fixation of alternative alleles. Both *S. s. sylvaticus* and *S. s. vohlynensis* differed from the other taxa by the following alleles:

Es-1^{100}, Es-2^{110}, Es-3^{100}, Es-10^{99}, Es-a^{100}, Hb-B^{100}, Ldh-B^{98}, Mod-1^{105}, Sod-1^{105}. The taxa identified as the "*microps*"-like displayed an alternative gene pool. The wood mouse from the Pamiro-Alay mountains, *S. s. pallipes*, can be characterized by fixation of some unique alleles (Es-$1^{93,96}$, Es-$2^{99,102}$, $Tf^{97.5,99.5}$, Idh-$1^{95.5}$), subspecies differing from other representatives of the "*microps*"-like species group.

Discussion

The analysis of genetic divergence among *S. sylvaticus* subspecies showed two main taxa groups at a species level of differentiation. One of them consists of the nominative *S. s. sylvaticus* (L.) and the *S. s. vohlynensis* at a very low level of divergence. Gene pools of these taxa are characterized by three alleles unique for the *Sylvaemus* genera, Sod-1^{105}, Mod-1^{105}, and Ldh-B^{98} having an identification significance for *S. sylvaticus* (L.) in Europe (Engel et al. 1973; Benmehdi et al. 1980; Csaikl et l. 1980; Csaikl 1983; Gemmeke 1980, 1983; Nascetti and Filippucci 1984; Gebczynsky et al. 1986; Britton-Davidian et al. 1991; Filippucci 1993; Hartl et al. 1992).

Comparison of data from the literature concerning *S. microps* diagnostic loci (Csaikl et al. 1980; Csaikl 1983; Gemmeke 1983; Filippucci 1993; Hartl et al. 1992) and pairwise comparison of gene pool in *S. sylvaticus* – *S. microps* do not contradict one another in principle. According to data in the literature (Csaikl et al. 1980; Csaikl 1983; Gemmeke 1983; Filippucci 1993), *S. microps* does not have unique alleles that can identify this species from the other representatives of wood mice genera. Only on the basis of diagnostic loci in pairwise comparisons can real diagnostics be achieved for *S. microps*. According to the presented data, all the "*microps*"-like taxa are characterized by two well-defined identification loci with fixations of Hb-B^{115} and Es-$a^{100.5}$ alleles. From the methodical point of view, these suitable loci were not studied by previous investigators (Csaikl et al. 1980; Gemmeke 1983; Filippucci 1993).

The second group of taxa, including also nominative *S. microps*, is characterized by relatively high levels of genetic differentiation even at significant levels for interspecies comparisons. Therefore, Pamiro-Alay *S. s. pallipes* can be divided from the other investigated subspecies identified as *S. microps*.

Specimens of the Pamiro-Alay taxon *S. s. pallipes* can be identified on the basis of some unique allelic variants of investigated loci: Es-$1^{93,94}$, Es-$2^{99,102}$, Idh-$1^{95.5}$, $Tf^{97.5,99.5}$. Thus, results presented here on genetic differentiation support taxonomic distinctness of *S. s. pallipes* at the allospecies level. Special interest, in addition to the Pamiro-Alay wood mice taxa, should be given to the most oriental wood mouse form, *S. s. kastschenkoi*, dwelling in the Altai. Earlier it was found (Mezhzherin and Michailenko 1991) that specimens of this subspecies are characterized by two diagnostic loci coding nonspecific esterases, and which have been excluded from sample of loci in this publication. This fact confirms a small but significant level of genetic distinctness of *S. s. kastschenkoi*.

The present results, confirming species identity of oriental wood mouse subspecies with *S. microps*, are not surprising if we refer to some earlier publications devoted to the systematics of *S. sylvaticus* in its oriental range. Firstly, Kratochvil and Rosicky (1952) in their descriptions of *S. microps* assumed that wood mice of Tataria (*S. s. mosquensis*), the southeastern Russia (*S. s. ciscaucasicus*), and Turkestan (*S. s. microtis*) are identical to this species. Zimmermann (1962) also presented data supposing that the traditional range of *S. sylvaticus* would be included in the range of *S. microps*. Crossings during 6 generations performed by Steiner (1979) have confirmed the presence of *S. microps* in northeastern Turkey. Moreover, on the basis of some morphological features he hypothesized that this species occurs in the Transcaucasus region and the mountainous areas of the Crimea.

An analysis of variation of morphological characters and some genetic features of occidental *S. sylvaticus* subspecies from the European part of the former USSR has found

that the subspecies, *S. s. uralensis* Pallas, 1811, is the oldest available name for a group of *S. microps*-like forms (Vorontzov et al. 1992). Further investigations of the southern Ural (type locality "*uralensis*") including data about central Asian taxa (Mezhzherin 1996) may confirm this point of view.

Acknowledgements

The author is grateful to A. G. Michailenko, N. N. Tovpinetz, S. I. Zolotuhina, E. I. Kotenkova, G. G. Boyeskorov, M. R. Ahverdjan, V. N. Peskov who collected specimens of wood mice as well as to N. N. Vorontzov for discussions. This investigation is supported by grant U-56000 of International Sciences Foundation (ISF) established by J. Soros.

Zusammenfassung

Biochemische Systematik der Waldmaus Sylvaemus sylvaticus (L., 1758) sensu lato (Rodentia, Muridae) aus Osteuropa und Asien

Mittels der elektrophoretischen Untersuchung von 36 Allozymloci wurde die taxonomische Zugehörigkeit der östlichen Unterarten von *Sylvaemus sylvaticus* überprüft. Fast alle östlichen Unterarten von *S. sylvaticus* (*charkovensis*, *baessleri*, *mosquensis*, *ciscaucasicus*, *uralensis*, *tsherga*, *pallipes*) wurden als der Spezies *Sylvaemus microps* s. l. zugehörig identifiziert. Lediglich *S. s. vohlynensis* ist nach wie vor der Art *S. sylvaticus* zuzuordnen. Die am weitesten im Osten vorkommenden Waldmäuse, *kastschenkoi* im Altaigebirge und *pallipes* in Tadjikistan, sind von der Nominatform *S. microps* durch mehrere fixierte allelische Unterschiede abzugrenzen. Derartige Unterschiede kennzeichnen sehr häufig verschiedene Arten. Die Subspezies *uralensis* Pallas, 1811 kann als ältestes valides Taxon innerhalb der Spezies *S. microps* gelten.

Literature

Bonhomme, F.; Catalan, J.; Britton-Davidian, J.; Chapman, V. M.; Moriwaki, K.; Nevo, E.; Thaler, L. (1984): Biochemical diversity and evolution in the genus *Mus*. Biochem. Genet. **22**, 275–303.

Benmehdi, F.; Britton-Davidian, J.; Thaler, L. (1980): Premier rapport de la genetique biochimique des population a la systematique des mulots de France continentale et de Corse. Biochem. Syst. Ecol. **8**, 309–315.

Britton-Davidian, J.; Vahdati, M.; Benmehdi, F.; Gros, P.; Nance, V.; Croset, H.; Guerassimov, S.; Triantaphyllidis, C. (1991): Genetic differentiation in four species of *Apodemus* from Southern Europe: *A. sylvaticus*, *A. flavicollis*, *A. agrarius*, and *A. mystacinus* (Rodentia, Muridae). Z. Säugetierkunde **56**, 25–33.

Csaikl, F.; Engel, W.; Schmidtke, J. (1980): On the biochemical systematics of three *Apodemus* species. Comp. Biochem. Physiol. **65 B**, 411–414.

Csaikl, F. (1983): Die Bedeutung von Isoenzymuntersuchungen für Systematik und Taxonomie der *Sylvaemus* (Rod., Mur., *Apodemus*). BFB-Bericht **47**, 225–237.

Davis, D. J. (1964): Disc-electrophoresis. Method and application to human serum proteins. Ann. N. Y. Acad. Sci. **121**, 404–427.

Engel, W.; Vogel, I.; Voiculescu, I.; Ropers, H. H.; Zenzes, M. T.; Bender, K. (1973): Cytogenetic and biochemical differences between *Apodemus sylvaticus* and *Apodemus flavicollis*, possibly responsible for the failure to interbreed. Comp. Biochem. Physiol. **44 B**, 1165–1173.

Filippucci, M. G.; Simson, S.; Nevo, E. (1989): Evolutionary biology of the genus *Apodemus* Kaup, 1829 in Israel. Allozymic and biometric analyses with description of a new species: *Apodemus hermonensis* (Rodentia, Muridae). Boll Zool. **56**, 361–376.

Filippucci, M. G. (1993): Allozyme variation and divergence among European, Middle Eastern, and North African species of the genus *Apodemus* (Rodentia, Muridae). Isr. J. Zool. **38**, 193–218.

Gebczynski, M.; Nielsen, J. T.; Simonsen, V. (1986): An electrophoretic comparison between three sympatric species of rodents from Jutland, Denmark. Hereditas **104**, 55–59.

Gemmeke, H. (1980): Proteinvariation und Taxonomie in der Gattung *Apodemus* (Mammalia, Rodentia). Z. Säugetierkunde **45**, 348–365.

GEMMEKE, H. (1983): Proteinvariation bei Zwergwaldmäusen (*Apodemus microps* Kratochvil und Rosicky, 1952). Z. Säugetierkunde **48**, 155–160.

HARTL, G. B.; SUCHENTRUNK, F.; WILLING, R.; MARKOWSKI, J.; ANSORGE, H. (1992): Inconsistency of biochemical evolutionary rates affecting allozyme divergence within the genus *Apodemus* (Muridae: Mammalia). Biochem. Syst. Ecol. **20**, 363–372.

ISKANDAR, D.; BONHOMME, F. (1984): Variabilite electrophoretique totale a 11 loci structuraux chez les rongeurs murids (Muridae, Rodentia). J. Genet. Cytol. **26**, 622–627.

KRATOCHVIL, J.; ROSICKY, B. (1952): K binomii a taxonomii mysi rodu *Apodemus microps.* Zool. entomol. Listy. **1**, 57–70.

MEZHZHERIN, S. V. (1987): Genetic divergence of wood mice of the subgenus *Sylvaemus.* Doklady Akademii Nauk SSSR **286**, 1255–1257 (In Rus.).

MEZHZHERIN, S. V. (1990): Allozyme variation and genetic divergence of wood mice of the subgenus *Sylvaemus* (Ognev et Vorobiev). Genetica **26**, 1046–1054 (In Rus.).

MEZHZHERIN, S. V. (1991): On the species distinctness of *Apodemus* (*Sylvaemus*) *ponticus* (Rodentia, Muridae). Vestnik zoologii N **6**, 34–40 (In Rus.).

MEZHZHERIN, S. V. (1992): Comparative analysis of allozyme variation of vertebrate animals. Zhurnal Obschey Biologii **53**, 549–556 (In Rus.).

MEZHZHERIN, S. V. (1996): Genetic relationships and systematical identity of Pamiro-Alay wood mouse *Apodemus sylvaticus pallipes* (Rodentia, Muridae). Biology Bulletin N **1**, 30–39.

MEZHZHERIN, S. V.; ZAGORODNJUK, I. V. (1989): A new species of mise of the genus *Apodemus* (Rodentia, Muridae). Vestnik zoologii N **4**, 55–59 (In Rus.).

MEZHZHERIN, S. V.; MICHAILENKO, A. G. (1991): On the species identity of Altai wood mouse, *Apodemus sylvaticus kastschenkoi* (Rodentia, Muridae). Vestnik zoologii N **3**, 35–44(In Rus.).

MEZHZHERIN, S. V.; ZYKOV, A. E. (1991): Genetic divergence and allozyme variation of mice of the genus *Apodemus* s. lato (Muridae, Rodentia). Tsitologia i genetica **25**, 51–58 (In Rus.).

MEZHZHERIN, S. V.; BOESKOROV, G. G.; VORONTZOV, N. N. (1992): Genetic relationship of European and Transcaucasus mice of the genus *Apodemus* Kaup. Genetica **28**, 111–121 (In Rus.).

MEZHZHERIN, S. V.; LASHKOVA, E. I. (1992): Diagnostics, geographic variation and distribution of two similar mice species *Sylvaemus sylvaticus* and *S. flavicollis* (Rodentia, Muridae). Vestnik zoologii N **3**, 33–41. (In Rus.).

NASCETTI, G.; FILIPPUCCI, M. G. (1984): Variabilita'e divergenza genetica in popolazioni italiane di *Apodemus sylvaticus* e *Apodemus flavicollis* (Rodentia, Muridae). Selvaggina **9**, 75–83.

NEI, M. (1975): Molecular population genetics and evolution. Amsterdam, North-Holland, Pub. Pp. 275.

NEI, M. (1978): Estimation of average heterozygosity and genetic distance from a small number of individuals. Genetics **89**, 583–590.

NEVO, E.; BEILES, A.; BEN-SHLOMO, R. (1984): The evolutionary signficance of genetic diversity: ecological, demographic and life history correlates. Lecture Notes in Biomathematics **53**, 13–213.

PEACOCK, A. C.; BUNTING, S. L.; QUEEN, K. G. (1965): Serum protein electrophoresis in acrylamide gel patterns from normal human subject. Science **147**, 1451–1455.

STEINER, H. M. (1979): Taxonomical status and geographical distribution of *Apodemus microps* Kratochvil et Rosicky, 1952. Zoologycheskiy zhurnal **58**, 1430–1432 (in Rus.).

STORCH, G.; LÜTT, O. (1989): Artstatus der Alpenwaldmaus, *Apodemus alpicola* Heinrich, 1952. Z. Säugetierkunde **54**, 337–346.

VOGEL, P.; MADDALENA, T.; MABILE, A.; PAQUET, G. (1992): Cofirmation biochimique du statut specifique du mulot alpestre *Apodemus alpicola* Heinrich, 1952 (Mammalia, Rodentia). Bull. Soc. Vaud. Sc. Nat. **80**, 471–481.

VORONTZOV, N. N.; MEZHZHERIN, S. V.; BOYESKOROV, G. G.; LYAPUNOVA, E. A. (1989): Genetic differentiation of sibling species of wood mice (*Apodemus*) from Caucasus and its diagnostics. Doklady Akademii Nauk SSSR **309**, 1234–1238 (In Rus.).

VORONTZOV, N. N.; BOESKOROV, G. G.; MEZHZHERIN, S. V.; LYAPUNOVA, E. A.; KANDAUROV, A. S. (1992): Systematics of wood mice of the subgenus *Sylvaemus* of Caucasus (Mammalia, Rodentia, *Apodemus*). Zoologycheskiy zhurnal **71**, 19–131. (In Rus.).

ZIMMERMANN, K. (1962): Die Untergattungen der Gattung *Apodemus* Kaup. Bonn. Zool. Beitr. **13**, 198–208.

Author's address: SERGEY S. MEZHZHERIN, Schmalhausen Institute of Zoology, Academy of Science, 252601-UA, Kiev, Ukraine

Z. Säugetierkunde **62** (1997) 312–314

ZEITSCHRIFT FÜR
SÄUGETIERKUNDE
INTERNATIONAL JOURNAL
OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNG

The karyotype of *Hemiechinus auritus calligoni* from Turkey

By H. Kefelioğlu

Department of Biology, Ondokuz Mayis University, Samsum, Turkey

Receipt of Ms. 06. 12. 1996
Acceptance of Ms. 10. 04. 1997

The long-eared hedgehog *Hemiechinus auritus* (Gmelin, 1770) is characterised not only by its phenotypic variability, but also by a chromosomal polymorphism. Despite this interest fact, little attempt has been made thus far to determine the extent by which the conventional subspecies correspond with the different chromosomal races. This species is of very marginal occurrence in Turkey, from whence two subspecies have been recognised to date: *H. a. dorotheae* Spitzenberger, 1978, from Cyprus is probably a human introduction (Boye 1991), whilst *H. a. calligoni* (Satunin, 1901) is considered to occur in south-eastern Anatolia, Iraq, Syria and Jordan (Harrison and Bates 1991). The aim of this study is to describe the chromosome set in material that is topotypical with *H. a. calligoni* (type locality is Aralik (Iğdir) on the Turkish-Iranian border).

Three specimens were collected between 1991–1993 in eastern Turkey: a male and a female at Aralik (Iğdir), and a female at Gaziantep. Standard flame-dried chromosome preparations were made directly from the bone marrow of colchicine-treated animals (Ford and Hamerton 1956). Ten slides were studied for each specimen, with at least 50 metaphase cells being examined. Chromosomal nomenclature follows Levan et al. (1964).

In all three specimens the diploid chromosome number was $2n = 48$, the fundamental chromosome number $NF = 94$, and the number of autosomal arms $NFa = 90$. Four groups of autosomes were recognised: (1.) ten metacentrics, (2.) seven submetacentrics, (3.) five subtelocentrics, and (4.) one small acrocentric (Fig. 1). The largest pair of autosomes was subtelocentric (pair 18 in Fig. 1), followed by two pairs of large metacentrics (pairs 1 and 2, respectively). The karyotype is also characterised by two pairs of very small autosomes (numbers 10 and 17 in Fig. 1). The X chromosome was metacentric, and the Y chromosome was a very small metacentric.

The diploid number of 48 chromosomes was also found in the other long-eared hedgehog populations studied so far, and is widespread in the entire family Erinaceidae, *Erinaceus amurensis* being the only exception (Zima and Král 1984). Despite this, the long-eared hedgehog does show inter-population differences in the position of the centromere. Orlov (1969) reported only bi-armed autosomes in the karyotype of *H. auritus* from Dagestan. This included a pair of very large subtelocentrics, two pairs of metacentrics, and two pairs of very small bi-armed chromosomes. The X chromosome was metacentric, and the Y chromosome was bi-armed and very small. Gropp et al. (1969) reporting on long-eared hedgehogs from Afghanistan and Egypt, also found a very large pair of subtelocentrics, two pairs of large metacentrics, and two pairs of very small metacentrics. Of the remaining autosomes, all 18 pairs were bi-armed (meta- to submetacentric) in Afghanistan animals, whilst there were 17 bi-armed pairs in hedgehogs from Egypt. No interpopulational differences exist in the heterosomes: the X is submetacentric, and the Y is very

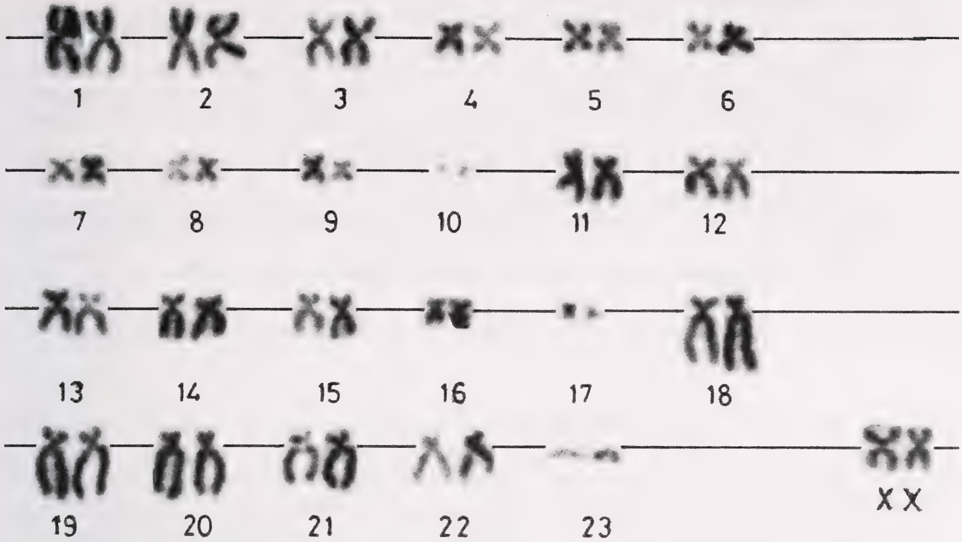


Fig. 1. Standard karyotype of a female *Hemiechinus auritus calligoni* from Aralik, Turkey.

small and bi-armed. The karyotype of Iraqi long-eared hedgehogs is characterised by a pair of very large subtelocentrics and two pairs of very small metacentrics. Of the remaining 38 autosomes, four pairs were subtelocentric and the rest were metacentrics. The X chromosome was metacentric and the Y chromosome was very small and bi-armed. Similar results were found also in populations from India (Sharma et al. 1975; Sobti and Gill 1980) and Turkmenistan (Zima and Kral 1984).

A pair of acrocentrics seems to be peculiar to long-eared hedgehogs from eastern Turkey, not having been found elsewhere. Furthermore, of the two pairs of very small autosomes (pairs 10 and 17 in Fig. 1), one was metacentric and the other was subtelocentric. Sharma et al. (1975), Sobti and Gill (1980), and Zima and Král (1984) all consider both to be metacentrics.

Harrison and Bates (1991) ascribed Iraqi *Hemiechinus auritus* to the subspecies *calligoni*. Karyological evidence does not support this step because of differences in the autosome morphology between Iraqi and Turkish long-eared hedgehogs. The karyotype found in topotypes of *H. a. calligoni* is known presently only from eastern Turkey.

Acknowledgements

I thank Dr. Boris Kryštufek for critical comments on an earlier draft of the study. Dr. Huw I. Griffiths kindly improved English and style.

References

Boye, P. (1991): Notes on the morphology, ecology, and geographic origin of the Cyprus long-eared hedgehog (*Hemiechinus auritus dorotheae*). Bonn. zool. Beitr. **42**, 115–123.

Ford, C. E.; Hamerton, J. L. (1956): A colchicine, hypotonic citrate, squash sequence for mammalian chromosomes. Stain Technol. **31**, 247–251.

Gropp, A.; Citoler, P.; Geisler, M. (1969): Karyotyp-variation und Heterochromatinmuster bei Igeln (*Erinaceus* und *Hemiechinus*). Chromosoma (Berlin) **27**, 288–307.

Harrison, D. L.; Bates, P. J. J. (1991): The mammals of Arabia. 2nd ed. Sevenoaks: Harrison Zool. Museum Publ.

Levan, A.; Fredga, K.; Sandberger, A. (1964): Nomenclature for centromeric position on chromosomes. Hereditas **52**, 201–202.

Orlov, V. N. (1969): Chromosome complement of the hedgehogs from East Europe. In: Mat. II. vsesoj. sov. po mlekopit. Ed. by N. N. Vorontsov. Pp. 6–7. (In Russian).

Sharma, G. P.; Mittal, O. P.; Sobti, R. C. (1975): Karyotype and chiasma frequency in the Indian hedgehog, *Hemiechinus auritus collaris*. Caryologia **28**, 149–156.

Sobti, R. C.; Gill, S. S. (1980): Chromosome number in fifteen mammals from India. Mamm. Chrom. Newsletter **21**, 107.

Zima, J.; Král, B. (1984): Karyotypes of European mammals I. Acta Sc. Nat. Brno **18**, 1–51.

Author's address: Dr. Haluk Kefelioğlu, Department of Biology, Ondokuz Mayis University, 55139 Kurupelit, Samsum, Turkey

Z. Säugetierkunde **62** (1997) 315–317

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Karyotypic status of shrews (*Sorex*) from Thrace, European Turkey

By J. Zima, Lenka Slivková, M. Andreas, P. Benda, and A. Reiter

Institute of Animal Physiology and Genetics, Academy of Sciences of the Czech Republic, Brno and Department of Zoology, Faculty of Science, Charles University, Prague, Czech Republic

Receipt of Ms. 06. 12. 1996
Acceptance of Ms. 10. 04. 1997

The mountain range of Istranca (Yıldız Dağlari) is situated in the easternmost tip of the Balkan peninsula, between the Black Sea and the Sea of Marmara. The area represents the south-eastern distribution limit of the forest fauna in Europe. The geographic proximity of Bosporus, where a land bridge existed at the end of the Pleistocene (Hosey 1982), has evoked ideas of dispersal of certain mammals of Asian origin into the area of Thrace and adjacent parts of the Balkans. Şimşek (1986) proposed the presence of the Caucasian common shrew, *Sorex satunini*, and described a new subspecies *S. satunini sultanae* from Istranca. *Sorex araneus* was not included, consequently, in the current list of the extant mammals of Turkey (Doğramaci 1989), and the Istranca Mts. did not appear within the European distribution range of the species (Hausser et al. 1990). Similarly, the presence of another Caucasian shrew, *S. volnuchini*, could be presumed in the easternmost parts of the Balkans.

In this study, we have examined the karyotype of shrews of the genus *Sorex* from Istranca to reveal their actual taxonomic status. The chromosomes represent a particularly appropriate character for such a study, because distinct differences in the karyotype structure are known both between *S. araneus/S. satunini* and *S. minutus/S. volnuchini*, respectively (Zima and Král 1984, for a review).

The karyotype was examined in six shrews collected in May 1992 and August 1996. The material studied included three common shrews (2 F, 1 M) and three lesser shrews (1 F, 2 M). All the specimens originated from Veliki Köprüsü bridge, approximately 8 km SW of Demirköy, Kirklareli District, 27°30′ E 41°40′ N (the type locality of *Sorex satunini sultanae*). Chromosome preparations were made by a standard method of direct treatment of bone marrow and spleen cells. The preparations were aged and then G-banded. The specimens examined were preserved as skulls and skins, or in alcohol, in the collection of the Department of Zoology, Charles University in Prague.

The karyotype of all the lesser shrews contained 42 chromosomes. The chromosome complement was identical to that reported in a number of populations of *S. minutus* in continental Europe and Asia (Zima and Král 1984).

The karyotype of all the common shrews contained 24 autosomes and the composite sex chromosomes XX or XY_1Y_2. In the autosomal set, there were two large biarmed pairs (arm combinations af, bc), one small metacentric pair (tu), and three biarmed Robertsonian pairs (ik, jl, mn). The other autosomes were acrocentric (Fig. 1). This karyotype demonstrates that the studied individuals belong indisputably to *S. araneus*. However, the composition of the Robertsonian fused autosomes is quite unique among the *S. araneus* populations studied so far (Zima et al. 1996). Therefore, we describe here a new chromosome race.

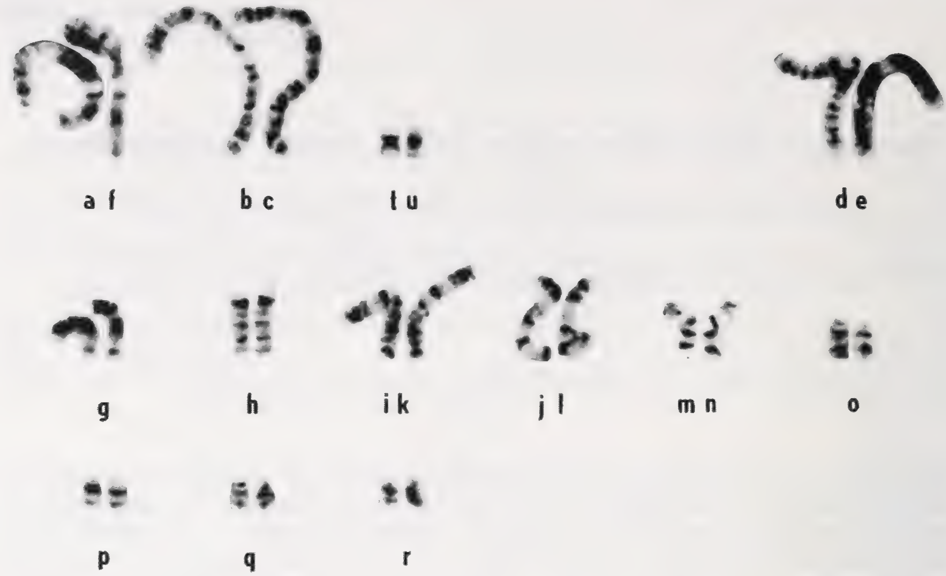


Fig. 1. The G-banded karyotype of a female of *Sorex araneus* from Istranca.

Istranca race: XX/XY_1Y_2, af, bc, g, h, ik, jl, mn, o, p, q, r, tu;

Type locality: Veliki Köprüsü bridge, Istranca Mts., Thrace, European Turkey, 27°30′ E 41°40′ N;

Distribution: The type locality, probably suitable habitats in higher altitudes all over the Istranca Mts.

The position of the Istranca race within the known karyotype races of *S. araneus* is apparently rather isolated. Most of the populations studied in Europe have a karyotype with the Robertsonian metacentrics gm, hi, jl, and they are usually included into the Western European Karyotypic Group, WEKG (Searle 1984; Wójcik 1993). The isolated position of the Istranca race in Europe seemed to be confirmed also in a mt DNA study (Mirol 1996).

Until now, the ik and mn metacentrics were found, along with other autosomal fusions, only in certain races described in north-eastern Poland, and included in the Eastern European Karyotypic Group, EEKG (Wójcik 1993; Fedyk 1995), and in four Siberian races (Král and Radjabli 1974; Aniskin and Volobouev 1981). It is obviously improbable that the fusions ik and mn could spread in Thrace through dispersal from north-eastern Poland or even from Siberia. The areas between Istranca and Poland are populated by races with karyotypes belonging to the WEKG (Zima et al. 1996). The finding from Istranca thus strongly indicates the real existence of the independent origin of the same autosomal fusions in different geographical populations of *S. araneus*.

Acknowledgements

We wish to thank Mgr. Jovana Čiháková and Mgr. M. Uhrin for their help in the field work. Professor C. Kurtonur helped us in organization of the field expeditions. Dr. J. B. Searle kindly read through the first draft of the manuscript. This study was supported by grants Nos. 204-93-0531 (GA CR) and A6045601 (GA AS CR).

References

ANISKIN, V. M.; VOLOBOUEV, V. T. (1981): Chromosomal polymorphism in Siberian populations of the shrews of *araneus-arcticus* complex (Insectivora, Soricidae). III. Three chromosomal forms of the common shrew *Sorex araneus* L. Genetika (Moscow) **17**, 1784–1791. [In Russian, with English summary].

DOĞRAMACI, S. (1989): The mammalian fauna of Turkey. Ondokuz Mayıs Üniv. Fen Dergisi **1**, 107–136. [In Turkish, with English summary].

FEDYK, S. (1995): Geographic chromosomal differentiation and hybrid zones between chromosome races of *Sorex araneus* in north-eastern Poland. Diss. Univ. Varsoviensis 439, Białystok. [In Polish, with English summary].

HAUSSER, J.; HUTTERER, R.; VOGEL, P. (1990): *Sorex araneus* Linnaeus, 1758 – Waldspitzmaus. In: Handbuch der Säugetiere Europas. Band 3/1. Insektenfresser – Insectivora, Herrentiere – Primates. Ed. by J. NIETHAMMER and F. KRAPP. Wiesbaden: AULA-Verlag. Pp. 237–278.

HOSEY, G. R. (1982): The Bosporus land-bridge and mammal distribution in Asia Minor and the Balkans. Säugetierkdl. Mitt. **30**, 53–62.

KRÁL, B., RADJABLI, S. I. (1974): Banding patterns and Robertsonian fusion in the western Siberian population of *Sorex araneus* (Insectivora, Soricidae). Folia Zool. **23**, 217–227.

MIROL, P. M. (1996): Molecular phylogenies and karyotypic evolution in small mammals: the examples of *Sorex araneus* in Eurasia and *Ctenomys* in South America. D. Phil. thesis, Univ. York.

SEARLE, J. B. (1984): Three new karyotypic races of the common shrew *Sorex araneus* (Mammalia: Insectivora) and a phylogeny. Syst. Zool. **33**, 184–194.

ŞIMŞEK, N. (1986): A new subspecies of *Sorex caucasicus* (Mammalia: Insectivora) from Turkey. DOĞA Tr. J. Biol. **10**, 206–208.

WÓJCIK, J. M. (1993): Chromosome races of the common shrew *Sorex araneus* in Poland: a model of karyotype evolution. Acta theriol. **38**, 315–338.

ZIMA, J.; FEDYK, S.; FREDGA, K.; HAUSSER, J.; MISHTA, A.; SEARLE, J. B.; VOLOBOUEV, V. T.; WÓJCIK, J. M. (1996): The list of the chromosome races of the common shrew (*Sorex araneus*). Hereditas **125**, 97–107.

ZIMA, J.; KRÁL, B. (1984): Karyotypes of European mammals I. Acta Sc. nat. Brno **18**, 1–51.

Authors' addresses: Dr. JAN ZIMA, Mgr. LENKA SLIVKOVÁ, Mgr. MICHAL ANDREAS, Mgr. PETR BENDA, and Mgr. ANTONÍN REITER, Department of Zoology, Charles University, Viničná 7, 128 44 Praha 2, Czech Republic.

Z. Säugetierkunde **62** (1997) 318–320

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Food of the Stone marten (*Martes foina*) in Nietoperek Bat Reserve

By P. Tryjanowski

Department of Avian Biology and Ecology, University of Poznań, Poznań, Poland

Receipt of Ms. 27. 11. 1996
Acceptance of Ms. 16. 04. 1997

Earlier sporadic studies on the food of the stone marten carried out in the 'Nietoperek' Bat Reserve created for preservation of bats suggested that bats could be the main component of the stone marten's diet (Urbańcyk 1981; Lesiński and Romanowski 1988). This report presents the results of an analysis of stone marten faeces from 'Nietoperek' and is an attempt to answer the question whether stone marten can limit the number of bats in the reserve.

Faecal samples were collected in underground fortifications, which are an ideal place for the hibernation of bats. More then 20,000 of bats belonging to 12 species regularly hibernate in the passages. The most numerous are *Myotis daubentoni* (12,500 individuals) and *M. myotis* (5,000 ind.). The species diversity and the number of bats are unusually high for Europe (Urbańcyk 1990).

The study of the stone marten diet is based on the analysis of 88 scats collected in March 1995 and March 1996. Prey was identified on the basis of bony remains and microscopic characteristics of hair. The prey biomass has been calculated using the coefficients of digestability according to Lockie (1961) and Goszcyński (1976): 118 for Cervidae carcass, 23 for small mammals (including bats), 35 for birds, 14 and 5 for fruits and insects, respectively. Food composition was expressed both in percent of biomass consumed and the percent of occurrence in scats, as the combination of these two measures provides a comprehensive view.

Results of the study are presented in table 1. The food of the stone marten from 'Nietoperek' is very diverse in regard to its quality.

Bats have been found in the food only three times (once *Plecotus auritus* and twice unidentified individuals). Both Urbańczyk (1981) and Lesiński and Romanowski (1988) observed a much greater amount of bats in the diet of stone marten in 'Nietoperek', even up to 81.3% of the dry food mass. Apart from 'Nietoperek' the stone marten preys on bats only sporadically and only one case of eating bats by marten is known for Romania (Romanowski and Lesiński 1991). Having made use of the two data gathered by the present author, as well as those of Lesiński and Romanowski (1988) and Urbańczyk (1981) one could state that the stone marten does not chose its preys at random (Tab. 2) – $\chi^2 = 532.5$ ($p < 0.0001$). The most numerous species – the Daubenton's bat *Myotis daubentoni* (Urbańczyk 1990), was not killed at all. The large amount of barbastelle bat *Barbastella barbastellus* could result from the fact that this species hibernates at the lowest level just above the ground and on the underground walls (Urbańczyk 1992) thus being the easiest prey.

The amount of the prey's rest is similar to the results presented by other authors (see review in Goszczyński 1977; Sumiński et al. 1993; Clevenger 1994; Lode 1994). Furthermore, the relatively high amount of fruits (wild rose, hawthorn, cherries, apples, berries) proves that the undergrounds are used by the stone marten at least since autumn. Percen-

Table 1. Food composition of the stone marten in 'Nietoperek' reserve. N = 226 prey item.

Item	% Occurrence	% Biomass
Microtus spp.	5.7	4.8
Rodents indet.	23.9	13.1
Sorex spp.	6.8	2.3
Chiroptera	3.4	6.2
Cervidae carcass	8	9.2
Aves	2.3	3.1
Insecta indet.	2.3	0.2
Grass	6.8	1.9
Seeds and fruits	71.6	58.8
Nonorganic matter	4.6	0.4

Table 2. Bat species found in marten food (data from Urbańczyk 1981, Lesiński and Romanowski 1988, this study – compiled) Explanations: N.win. – numbers of individuals wintering in "Nietoperek" reserve N.f. – numbers of individuals in marten food.

Species	N.win.	N.f.
Myotis myotis	5 000	33
Barbastella barbastellus	1 000	123
Plecotus auritus	800	2
Myotis nattereri	350	1

tage of fruit occurrence is similar to the data obtained from the Mediterranean habitats (Pandolfi et al. 1996). Data collected there point to a polyphagous character of the stone marten diet. The obtained data clearly show, however, that the stone marten poss a threat to bats' population.

Acknowledgements

I am indebted to A. Kujawa and A. L. Ruprecht for their expertise in identifing prey remains. I am very grateful to G. Kucharczyk, J. Ptaszyk, A. Zalewski, and R. Paszkiewicz for their comments on earlier versions of the manuscript.

References

Clevenger, A. P. (1994): Feeding ecology of Eurasian Pine Martens and Stone Martens in Europe. In: Martens, Sables, and Fishers. Biology and Conservation. Ed. by S. W. Buskirk, A. S. Harestad, M. G. Raphael, and R. A. Powell. London: Cornell Univ. Press. Pp. 326–340.

Goszczyński, J. (1976): Composition of the food of martens. Acta theriol. **21**, 527–534.

Goszczyński, J. (1977): Connections between predatory birds and mammals and their prey. Acta theriol. **22**, 399–430.

Lesiński, G.; Romanowski, J. (1988): Kuny polują na nietoperze. [Martens hunting on bats]. Wszechświat **89**, 210.

Lockie, J. D. (1961): The food of the pine marten *Martes martes* in West Ross-Shire, Scotland. Proc. Zool. Soc. Lond. **136**, 186–195.

Lode, T. (1994): Feeding habits of the Stone marten *Martes foina* and environmental factors in western France. Z. Säugetierkunde **59**, 189–191.

Pandolfi, M.; de Marinis, A. M.; Petrov, I. (1996): Fruit as a winter feeding resource in the diet of Stone marten (*Martes foina*) in east-central Italy. Z. Säugetierkunde **61**, 215–220.

Romanowski, J.; Lesiński, G. (1991): A note of the diet of stone marten in southeastern Romania. Acta theriol. **36**, 201–204.

Sumiński, P.; Goszczyński, J.; Romanowski, J. (1993): Ssaki drapieżne Europy. [Carnivores of Europe]. Warszawa: PWRiL.

Urbańczyk, Z. (1981): Fledermäuse (Chiroptera) in der Nahrung der Marders (*Martes* sp.). Säugetierkdl. Mitt. **29**, 77–79.

Urbańczyk, Z. (1990): Northern Europe's most important bat hibernation site. Oryx **24**, 30–34.

Urbańczyk, Z. (1992): Wintering biology and ecology of the barbastrelle *Barbastella barbastellus* (Schreber, 1774) (Mammalia: Chiroptera). Ph.D. diss., Univ. of Poznań [In Polish].

Author's address: Piotr Tryjanowski, Department of Avian Biology and Ecology, University of Poznań, Fredry 10, PL-61-710 Poznań, Poland.

Redaktionelle Hinweise

Einsendung und Annahme von Manuskripten: Ms. zur Veröffentlichung sind einzusenden an den 1. Schriftleiter: Herrn Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel. e-mail: dkruska@ifh.uni-kiel.de

Über die Annahme von Ms. zur Veröffentlichung wird gemäß Geschäftsordnung der Deutschen Gesellschaft für Säugetierkunde entschieden. Der Eingang von Ms. wird sofort bestätigt, und nach Erhalt der Gutachten werden die Autoren über die Entscheidung umgehend informiert.

Schriftwechsel, der die technische Drucklegung betrifft, ist zu richten an: Zeitschrift für Säugetierkunde, Gustav Fischer Verlag, Villengang 2, D-07745 Jena.

Äußere Form der Manuskripte: Die Ms. sind 3fach und vollständig als Original mit 2 Kopien in deutscher oder englischer Sprache einzureichen. Sie müssen mit Schreibmaschine oder als deutlich lesbare Computerausdrucke auf DIN A4-Blättern (21×29,7 cm), mit einem linken Heftrand von 4 cm und durchgehend mit einem doppelten Zeilenabstand geschrieben sein. Jedes Ms. soll auf der 1. Seite folgende Angaben enthalten: Titel der Studie; Name(n) der Autoren (männliche Vornamen nur in Initialen, weibliche ausgeschrieben); Institution(en), an der (denen) die Studie durchgeführt wurde. Ferner soll bei längeren Titeln ein kurzer Kolumnentitel (Seitenüberschrift) von maximal 72 Anschlägen angegeben werden.

Die Schrifttypen müssen einheitlich sein, ohne halbfette, gesperrte, kursive etc. Hervorhebungen. Fußnoten auf den Seiten oder Appendices am Ende sind nicht zugelassen. Autorennamen im Zusammenhang mit Literaturzitaten sind im Text mit Bleistift zu unterstreichen. Wissenschaftliche zoologische und botanische Gattungs-, Art- und Unterartnamen sind mit einer Schlangenlinie zu unterstreichen. Der Name von Erstbeschreibern bei wissenschaftlichen Namen wird nicht unterstrichen.

Im Ms. ist am Rand mit Bleistift zu vermerken, an welcher Stelle die einzelnen Abbildungen und Tabellen eingefügt werden sollen.

Am Ende der Studie, im Anschluß an das Literaturverzeichnis, sind die genauen postalischen Adressen des (der) Autoren anzugeben.

Umfang und Aufbau der Manuskripte: Manuskripte können als Originalarbeiten oder als wissenschaftliche Kurzmitteilungen veröffentlicht werden.

a) Originalarbeiten: Originalarbeiten sollen einschließlich Abbildungen, Tabellen und Literaturverzeichnis einen Gesamtumfang von 30 Ms.-Seiten nicht überschreiten. Der Text soll eine klare Gliederung aufweisen in: Abstract (in englischer Sprache), Einleitung, Material und Methode, Ergebnisse, Diskussion (oder zusammengefaßt als Ergebnisse und Diskussion), Danksagungen, Zusammenfassung und Literatur.

Bei deutschsprachigen Studien ist über dem englischen Abstract der Titel in englischer Sprache anzugeben. Bei englischsprachigen Studien ist entsprechend über der deutschen Zusammenfassung der Titel in deutscher Sprache anzugeben.

b) Wissenschaftliche Kurzmitteilungen: Wissenschaftliche Kurzmitteilungen sollen einen Gesamtumfang von 5 Ms.-Seiten nicht überschreiten. Sie enthalten kein Abstract und keine Zusammenfassung. Bei deutschsprachigen Ms. ist jedoch auf der 1. Seite zusätzlich eine englische Übersetzung des Titels anzugeben, bei englischsprachigen entsprechend eine deutsche Übersetzung. Wissenschaftliche Kurzmitteilungen sind äußerlich nicht in die Kapitel Einleitung, Material und Methode, Ergebnisse und Diskussion gegliedert, müssen aber in der textlichen Darstellung diese Strukturierung erkennen lassen.

Abbildungen: Anzahl und Größe der Abbildungen sind unbedingt auf das notwendige Mindestmaß zu beschränken. Es können nur kontrastreiche, reproduktionsfähige Originale verwendet werden, farbige Abbildungen werden nicht angenommen. Beschriftungen müssen einheitlich und wegen späterer Verkleinerung groß und kräftig sein. Auf der Rückseite sind laufende Numerierung, Zeitschrift und Autorennamen anzugeben. Alle Bildunterschriften sollen auf einem gesonderten Blatt gelistet werden.

Tabellen: Tabellen müssen auf ein Mindestmaß beschränkt werden. Jede Tabelle muß auf einem gesonderten DIN A4-Blatt angelegt sowie mit Überschrift und laufender Numerierung versehen sein. Umfangreichere Tabellen müssen auf Folgeblättern als Fortsetzung erscheinen.

Literaturverzeichnis: Jede zitierte Arbeit ist in alphabetischer Reihenfolge aufzuführen. Es soll nur international erreichbare Literatur zitiert werden. Die Zeitschriften werden mit ihrem Kurztitel angegeben.

Beispiele:

a) Zeitschriftenbeiträge:

Kalko, E. K. V; Handley, C. O. Jr. (1994): Evolution, biogeography, and description af a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá. Z. Säugetierkunde **59**, 257–273.

b) Bücher:

Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.

c) Handbuchbeiträge:

Niethammer, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

Drucklegung: Der jeweilige Hauptautor erhält sowohl die Andrucke der Bilder zur Prüfung wie auch den kompletten Umbruch seines Artikels zusammen mit dem Ms. Es dürfen nur tatsächliche Satzfehler korrigiert werden. Vom Ms. abweichende Änderungen werden dem Autor in Rechnung gestellt. Es sind die üblichen Korrekturzeichen zu verwenden. Ein als druckfertig bezeichneter Abzug ist zu senden an: Herrn Prof. Dr. Peter Langer, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität, Aulweg 123, D-35385 Giessen. e-mail: peter.langer@anatomie.med.uni-giessen.de

Sonderdrucke: Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen erhalten 50 Sonderdrucke gratis. Mehrbedarf kann gegen Berechnung bei Rücksendung des Umbruchs bestellt werden.

Publisher: Gustav Fischer Verlag GmbH & Co. KG, Branch Office Jena, P. O. Box No. 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/6 26-3; Fax ++49(0)36 41/62 65 00; e-mail: office.j@gfischer.de
Advertisement bookings: Enquiries should be directed to Gustav Fischer Verlag, Advertising Manager: Sabine Schröter, P. O. Box 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/62 64 28, Fax ++49(0)36 41/62 64 21
Advertising rates: The price list from February 1, 1997 is effective at present.
Distribution and subscription agency:
For customers **in the German speaking countries:** Please turn to your bookshop or to SFG-Servicecenter Fachverlage GmbH, Zeitschriftenvertrieb: Barbara Dressler, Villengang 2, D-07745 Jena, Germany. Phone ++49(0)36 41/62 64 44, Fax ++49(0)36 41/62 64 43;
For customers **in all other countries:** Please contact your bookshop or Stockton Press., c/o Debbie Floyd, The Subscription Dept., Houndmills, Basingstoke, Hants RG 21 6XS, UK. Phone ++44(0)12 56/35 18 98. Fax ++44/12 56/32 83 39. Subscribers in the **USA** can call toll free on ++1/800/747 3187.
Terms of delivery (1997): 1 volume consisting of 6 issues.
Subscription rate (1997): Price per volume: DM 398.00; ÖS 2 906.00; sFr 382.50; UK Sterling 183.00
Single issue price: DM 80.00; ÖS 584.00; sFr 77.00; UK Sterling 35.00
STOCKTON
Reduced membership rates are available on request. Please turn to our publ. house.
All prices mentioned above are exclusive postage. USdollar prices are converted at the current exchange rate. We accept the following credit cards: VISA/Mastercard/American Express, (Please note card-No. and expiry date).
Banking connections:
For customers in the **German speaking countries:**
Deutsche Bank AG Jena, Konto-Nr. 6 284 707, BLZ 820 700 00.
For costumers **in the other countries:**
UK Post Office Giro Account No. 5 192 455. Full details must accompany the payment.
All prices are subject to change without notice.
Subsciption information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting, printing and binding: druckhaus köthen GmbH
Printed in Germany

Printed on acid-free paper effective with vol. 61, no. 1, 1996.

Abstracted/Indexed in
Animal Breeding Abstracts; Current Contents Agriculture, Biology Environmental Sciences; Biological Abstracts; *BIOSIS* database; Current Advances in Ecological and Environmental Sciences; Dairy Science Abstracts; Fisheries Review; Helminthological Abstracts; Index Veterinarius; South Pacific Periodicals Index; Veterinary Bulletin; Key Word Index to Wildlife Research; Wild Review (Fort Collins); Zoological Record

ZEITSCHRIFT FÜR SÄUGETIERKUNDE

INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Organ der Deutschen Gesellschaft für Säugetierkunde

Beilage: Titel und Inhalt zu Band 62

GUSTAV FISCHER

ISSN 0044-3468
Z. Säugetierkunde
Jena · 62(1997)6 · S. 321-384
Dezember 1997

6
1997

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Z. Säugetierkunde 62 (1997) 321–329

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Das sekundäre Schultergelenk der Vespertilionoidea (Mammalia: Chiroptera)

Von H. Schliemann

Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Hamburg

Eingang des Ms. 29. 10. 1996
Annahme des Ms. 18. 03. 1997

Abstract

The secondary shoulder joint of the Vespertilionoidea

The morphology of the shoulder joint of *Natalus stramineus* (Natalidae), *Furipterus horrens* (Furipteridae), *Thyroptera tricolor* (Thyropteridae), *Myzopoda aurita* (Myzopodidae), and *Mystacina tuberculata* (Mystacinidae) is presented. These taxa belong to the superfamily Vespertilionoidea of which the shoulder joint has been investigated recently in members of the families Vespertilionidae and Molossidae. All the species studied here own a secondary shoulder joint which consists of an additional articular surface on the dorsal scapular aspect and an enlarged tuberculum majus. The findings show that all families of the Vespertilionoidea have a secondary shoulder joint which in this superfamily – as generally in the Microchiroptera – exhibits a remarkable morphological variation. Referring to the size of the additional articular surfaces, members of the families Molossidae and Vespertilionidae own the most differentiated secondary joint followed by the Mystacinidae and the Myzopodidae. The less differentiated shoulder joint in this superfamily is found in the Furipteridae with the Natalidae and the Thyropteridae ranging between Furipteridae on one hand and Myzopodidae and Mystacinidae on the other. The secondary shoulder joint is only one of the biomechanical devices developed by the Microchiroptera to reduce rotation movements of the humerus against the scapula during the wing's downstroke, the other one consisting of an elongated humeral head and a corresponding transformation of the cavitas glenoidalis scapulae. Both modifications of the basic morphology of the mammalian shoulder joint developed within the Microchiroptera several times independently in parallel evolution.

Einleitung

Das Schultergelenk der Säuger mit seinem halbkugeligen Humeruskopf und einer entsprechend gestalteten, vergleichsweise kleinen Cavitas glenoidalis der Scapula ist bei den meisten Microchiropteren abgewandelt. Die morphologischen Veränderungen lassen zwei verschiedene Richtungen erkennen: Der Humeruskopf wird entweder mehr oder weniger ausgeprägt in Richtung auf eine ovoide bis langgestreckte und proximal gratförmige Gestalt verändert, wobei die Cavitas glenoidalis eine korrespondierende Abänderung erfährt. Oder aber das Gelenk wird dadurch verändert, daß das auf seiner Innenseite mit Gelenkknorpel überzogene und vergrößerte Tuberculum majus mit einer zusätzlichen Gelenkfläche auf der Dorsalseite des Schulterblattes artikuliert und so ein sekundäres Gelenk bildet.

Während die zuerst genannte Form der Abwandlung bisher kaum Beachtung gefunden hat (Miller 1907; Smith 1972; Schlosser-Sturm und Schliemann 1995), ist das sekundäre Schultergelenk spätestens seit Miller (1907) morphologisch bekannt und hat sowohl unter funktionellen als auch systematischen Gesichtspunkten häufiger und mehr oder weniger

ausführlich Erwähnung in der Literatur gefunden (u. a. Weber 1928; Vaughan 1959; Schlosser-Sturm 1982; Koopmann 1995; Schlosser-Sturm und Schliemann 1995).

Beide Typen des abgewandelten Schultergelenks sind unter einem offenbar sehr starken funktionellen Zwang mehrmals unabhängig in paralleler Evolution entstanden, wobei sich jeder Typus in unterschiedlichen Ausprägungsgraden entwickelt hat (Schlosser-Sturm und Schliemann 1995). In diesem Zusammenhang ist von Interesse, daß das sekundäre Schultergelenk bei den Familien der Vespertilionoidea hoch entwickelt ist. Veränderungen des Schultergelenks im Sinne der zuerst genannten Abwandlung sind in dieser Gruppe nicht bekannt.

Bislang kennen wir den Bau des Schultergelenks unter den Vespertilionoidea allerdings nur bei den Vespertilionidae und den Molossidae. Jedenfalls ist das sekundäre Schultergelenk einzelner Arten aus diesen Familien exemplarisch beschrieben, und es wird auf Grund der erhobenen Befunde auf die morphologische Situation der jeweiligen Familien insgesamt rückgeschlossen. Dies ist wahrscheinlich im großen und ganzen berechtigt. Aber es muß eingestanden werden, daß wir über die Variabilität des Baues des sekundären Schultergelenks innerhalb der Familien nicht abschließend Bescheid wissen. Mit diesem Vorbehalt werden die nachfolgend geschilderten Befunde als familientypisch angesehen.

Untersuchungen über den Bau des Schultergelenks der Natalidae, Furipteridae, Thyropteridae, Myzopodidae und Mystacinidae stehen noch aus. Es gibt zwar mehrfach Hinweise in der Literatur (Miller 1907; Weber 1928; Koopman 1994; für Nataliden und Thyropteriden Strickler 1978), jedoch liegen bislang keine dokumentierten morphologischen Analysen vor. In der kürzlich erschienenen Darstellung des Schultergelenks der Chiropteren (Schlosser-Sturm und Schlieman 1995) konnten diese fünf Familien nicht berücksichtigt werden. Nachfolgend soll diese Lücke geschlossen werden.

Material und Methode

Von je einem Vertreter der Familien der Natalidae (*Natalus stramineus* Gray, 1838), Furipteridae (*Furipterus horrens* (Cuvier, 1828)), Thyropteridae (*Thyroptera tricolor* Spix, 1823), Myzopodidae (*Myzopoda aurita* Milne-Edwards und Grandidier, 1878) und Mystacinidae (*Mystacina tuberculata* Gray, 1848) wurden Scapula und proximale Epiphyse des Humerus einer Körperseite präpariert und von Muskelresten und dem Bindegewebe der Gelenkkapsel befreit. Sie wurden sodann unter Berücksichtigung der Ausdehnung des Gelenkknorpels mit Hilfe von Stereomikroskop und Zeichenspiegel maßstabsgerecht gezeichnet. Die morphologische Analyse beschränkt sich auf die Strukturen des Schultergelenks (Abb. 1). Ihre Beschreibung folgt der üblichen Terminologie (z. B. Norberg 1970), die bei Chiropteren von einer horizontal ausgestreckten Vorderextremität wie in der Mitte ihres Abschlags im Flug ausgeht. Dies bedeutet, daß die Oberseite der Schwinge ihre Dorsalseite ist, und daß die Dorsalseite des Humerus der lateralen der meisten anderen Säuger entspricht.

Die Exemplare aus den Familien Natalidae, Furipteridae und Mystacinidae stammen aus den Sammlungen des Naturmuseums Senckenberg/Frankfurt, die der Familien Thyropteridae und Myzopodidae aus dem Zoologischen Museum Hamburg.

Ergebnisse

Alle hier untersuchten Vertreter der Familien der Vespertilionoidea sind im Besitz einer sekundären Gelenkfläche auf der Dorsalseite der Scapula und eines Tuberculum majus humeri, das für die Artikulation mit dieser sekundären Gelenkfläche auf der Scapula auf seiner Innenseite mit Gelenkknorpel bedeckt ist. Im Detail ergeben sich in den Familien die folgenden morphologischen Eigenheiten.

Natalidae (Abb. 2 A)

Natalus besitzt eine Scapula mit unauffälliger Cavitas glenoidalis, die sich in cranialer Richtung beträchtlich verschmälert. Ihre ventrale Begrenzung verläuft mehr oder weniger in horizontaler Richtung, der dorsale Rand ist konkav nach ventral eingezogen, und der caudale Teil der Cavitas besitzt caudal und dorsal einen fast kreisrunden Umriß. Die sekundäre Gelenkfläche liegt dorsal des verschmälerten cranialen Anteils der Cavitas und ist deutlich mit aufgewölbten Rändern gegenüber ihrer Umgebung abgegrenzt. An die Cavitas glenoidalis grenzt sie geradlinig mit einem scharfen Grat. Ihre Fläche ist etwa rechtwinklig zur Gelenkfläche der Cavitas glenoidalis orientiert und nach medial konkav vertieft. Ihre Größe beträgt etwa ein Viertel der Größe der Cavitas. Die Tuberositas supraglenoidalis ist in Form eines kleinen Fortsatzes nur schwach ausgebildet.

Der Humeruskopf ist aus caudaler Sicht annähernd halbkugelig und verschmälert sich ein wenig auf der Proximalfläche. Das Caput wird vom Tuberculum majus deutlich in proximaler Richtung überragt. Tuberculum majus und ebenso das nach ventral ausladende aber schwach entwickelte Tuberculum minus laufen nach distal in breite Leisten aus. Die Vertiefung zwischen Caput und Crista pectoralis auf der Proximalfläche des Humerus ist seicht. Sie ist ebenso wie die Innenseite des Tuberculum majus und die Rinne zwischen Caput und Tuberculum majus mit Gelenkknorpel überzogen.

Furipteridae (Abb. 2 B)

Die Cavitas glenoidalis von *Furipterus* entspricht in Gestalt und Begrenzung der zuvor geschilderten von *Natalus.* Die sekundäre Gelenkfläche liegt ebenfalls dorsal des verschmälerten cranialen Teils der Cavitas. Beide Gelenkflächen sind durch einen deutlichen Grat voneinander getrennt. Dagegen ist die sekundäre Gelenkfläche in Richtung auf das Collum scapulae nicht sehr markant abgegrenzt. Und darüber hinaus ist sie nur geringfügig konkav vertieft und im Verhältnis zur Cavitas flächenmäßig weniger ausgedehnt als bei *Natalus.* Die Tuberositas supraglenoidalis ragt nicht auffallend weit nach lateral vor.

Das Caput humeri ist auf der ventralen Seite leicht abgeflacht, sein Längsdurchmesser, in Schaftrichtung liegend, daher etwas größer als der Querdurchmesser. Das Tuberculum majus überragt das Caput in proximaler Richtung. Das Tuberculum minus dieser Art ist ein auffallend kräftiges Gebilde, das allenfalls geringfügig über den Humeruskopf nach proximal hinausragt. Beide Tubercula laufen schaftwärts in die Crista tuberculis majoris bzw. Cr. t. minoris aus. Die Proximalfläche des Humerus ist kräftig skulpturiert, die Vertiefung hinter der Crista pectoralis dennoch seicht. Innenseite des Tuberculum majus, diese Vertiefung und tiefe Rinnen zwischen Caput und Tubercula sind mit Gelenkknorpel versehen.

Thyropteridae (Abb. 2 C)

Die Cavitas glenoidals von *Thyroptera* gleicht weitgehend denjenigen von *Natalus* und *Furipterus.* Allerdings läßt sich an diesem Präparat besser als bei den anderen erkennen, daß Dorsal- und insbesondere Ventralrand der Gelenkpfanne durch kräftige Knorpellippen überbaut sind. Die sekundäre Gelenkfläche auf der Dorsalseite der Scapula von *Thyroptera* ist deutlich konkav vertieft, klar abgegrenzt und relativ größer als bei den zuvor beschriebenen Arten. Sie besitzt eine Größe von reichlich einem Viertel der Größe der Cavitas glenoidalis. Bei dem vorliegenden Präparat des Schultergürtels von *Thyroptera* läßt sich ferner erkennen, daß in die sekundäre Gelenkfläche eine mit Gelenkknorpel überzogene Bandverbindung, ein Ligamentum coracoclaviculare, zwischen der Basis des Proc. coracoideus und dem Distalende der Clavicufa einbezogen ist. Hierdurch sowie durch die Tatsache, daß der Rand der sekundären Gelenkfläche zur Cavitas nach dorsal

aufgebogen ist, stellt die Oberfläche dieses zusätzlichen Gelenks eine tiefe Incisur dar, dem Ausschnitt einer Zylinderinnenwandung gleichend. Eine entsprechende topographische Beziehung zwischen Distalende der Clavicula und Basis des Proc. coracoideus läßt sich ebenfalls bei *Natalus*, nicht dagegen bei *Furipterus* feststellen. Die Tuberositas supraglenoidalis ist auch bei *Thyroptera* schwach entwickelt.

Der Humeruskopf besitzt einen ovalen Umriß mit schräg gestellter langer Achse, eine Situation, wie sie ebenfalls von anderen Vespertilionoidea (Vespertilionidae, Molossidae) beschrieben wurde. Das kräftige Tuberculum majus überragt das Caput humeri wiederum deutlich, das Tuberculum minus ist weniger kräftig entwickelt und wirkt im Vergleich mit den zuvor besprochenen Arten wie an das Caput herangerückt. Es endet proximal auf derselben Höhe wie das Caput. Die Vertiefung zwischen Crista pectoralis und Caput ist ausgeprägter als bei den zuvor besprochenen Arten. Die tiefe Furche zwischen Caput und Tuberculum majus ist ebenso wie die seichtere Furche zum Tuberculum minus hin und die Innenseite des Tuberculum majus mit Gelenkknorpel überzogen. Blickt man aus der Richtung des Caput auf die Innenseite des Tuberculum majus, so erkennt man, daß diese Fläche die Gestalt eines kräftigen eiförmigen Gelenkkopfes mit erheblicher Ausdehnung in rostrocaudaler Richtung aufweist. Dies ist bei *Thyroptera* wiederum deutlicher als bei *Furipterus* und *Natalus.*

Myzopodidae (Abb. 2 D)

Der Umriß der Cavitas glenoidalis entspricht den Verhältnissen, wie sie vorstehend für die anderen Arten beschrieben wurden. Auch bei dem vorliegenden Präparat des Schulterblattes von *Myzopoda* ist erkennbar, daß der ventrale Rand der Gelenkpfannne durch eine Knorpellippe vervollständigt wird. Die dorsale Gelenkfläche ist mit einem deutlichen knöchernen Wulst gegenüber der Umgebung abgegrenzt und nur mäßig konkav vertieft. Sie ist im Vergleich zur Cavitas glenoidalis eindeutig größer als bei den zuvor besprochenen Arten. Ihre Fläche umfaßt sicher ein Drittel derjenigen der Cavitas glenoidalis. Das Ligamentum coracoclaviculare ist in einiger Entfernung von der sekundären Gelenkfläche am Proc. coracoideus befestigt, so daß es nicht in den sekundären Gelenkapparat mit einbezogen ist. Die Tuberositas supraglenoidalis ist kräftig ausgebildet und steht markant nach lateral vor.

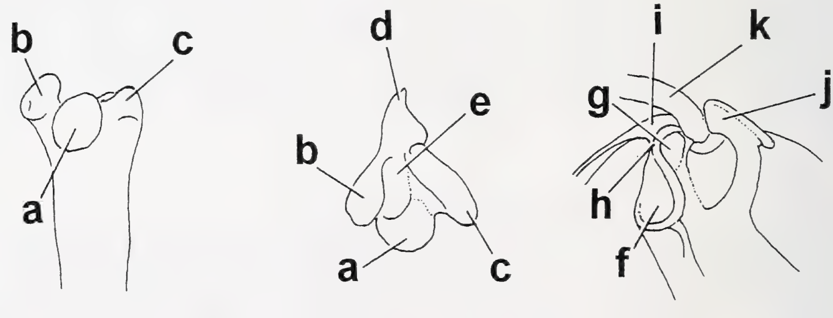
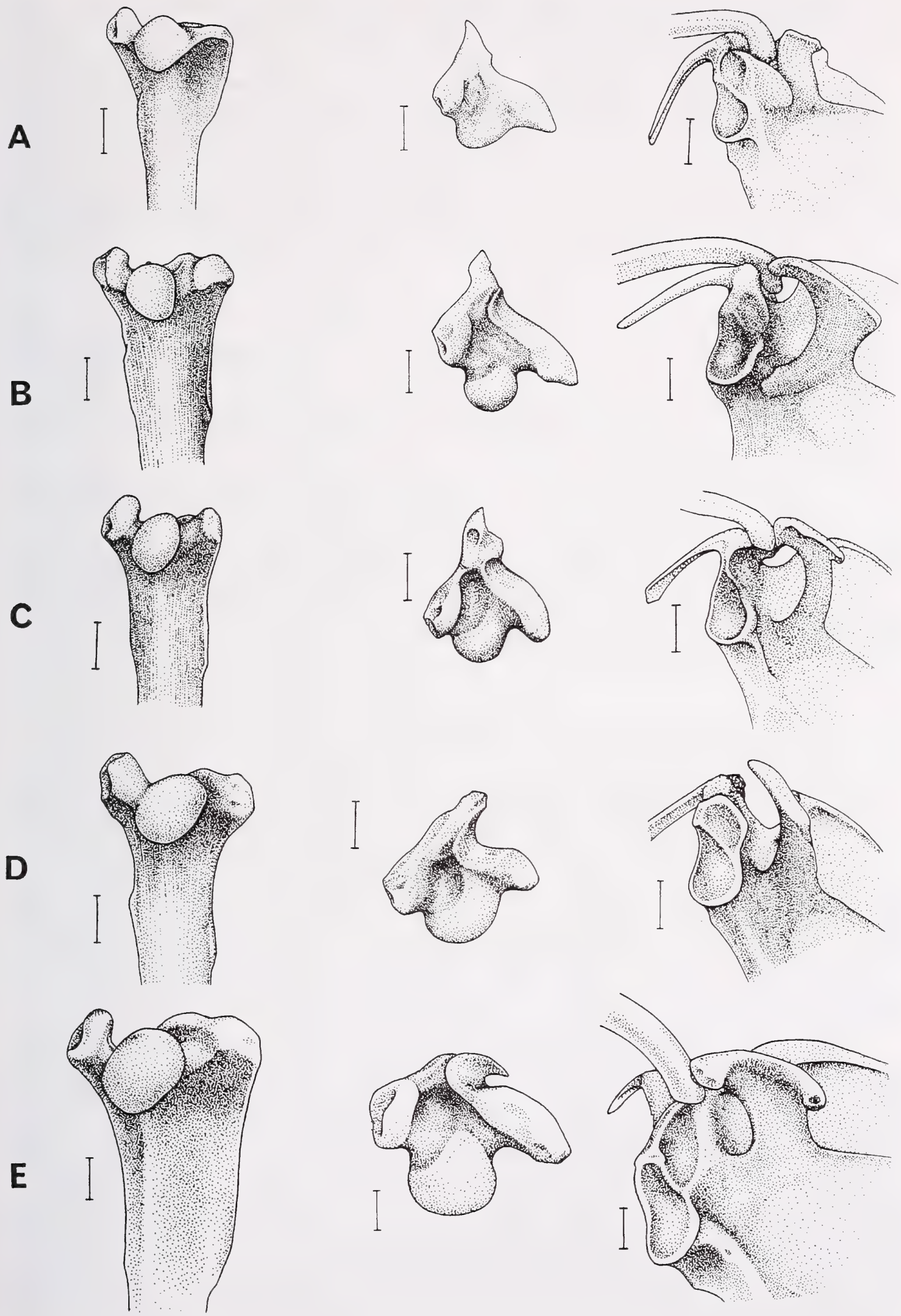


Abb. 1. Die Strukturen des Schultergelenks und seiner Umgebung a = Caput humeri, b = Tuberculum majus, c = Tuberculum minus, d = Crista pectoralis, e = Vertiefung auf der Proximalfläche des Humerus, f = Cavitas glenoidalis, g = sekundäre Gelenkfläche, h = Tubersositas glenoidalis, i = Proc. coracoideus, j = Acromion, k = Clavicula

▶

Abb. 2. Proximale Epiphyse des Humerus (links Ansicht von caudal, Mitte von proximal) und des rostrolateralen Teils der Scapula (rechts) von *Natalus stramineus* (A), *Furipterus horrens* (B), *Thyroptera tricolor* (C), *Myzopoda aurita* (D) und *Mystacina tuberculata* (E) (A rechte Körperseite, seitenverkehrt abgebildet; B, C, D und E linke Körperseite). Der Maßstab entspricht jeweils 1 Millimeter.


A
B
C
D
E

Das Caput humeri ist wiederum schräg zur Längsachse des Knochens gestellt und wird vom Tuberculum majus in proximaler Richtung weit überragt. Das Tuberculum minus überragt den Humeruskopf nicht und ist vergleichsweise schwächer entwickelt. Die grubigen Vertiefungen zwischen Caput und den Tubercula sind ebenso wie die Innenseite des Tuberculum majus mit Gelenkknorpel bedeckt. Allerdings ist diese Innenseite des Tuberculum majus bei weitem nicht so stark konvex gewölbt wie bei *Thyroptera*, was der auch nur leicht konkaven Vertiefung der sekundären Gelenkfläche auf der Scapula entspricht. Auch ist die rostrocaudale Ausdehnung des Tuberculum majus nicht dieselbe wie bei *Thyroptera*. Die Grube zwischen Caput und Crista pectoralis ist stark vertieft, so daß sie die kräftige Tuberositas supraglenoidalis aufzunehmen vermag.

Mystacinidae (Abb. 2E)

Die Scapula ist sehr robust, die Cavitas auffällig tief und mit hohen Knorpellippen ventral und im caudalen Bereich versehen. Die sekundäre Gelenkfläche ist groß und umfaßt wiederum etwa ein Drittel der Cavitasfläche. Auch bei *Mystacina* beteiligt sich das Lig. coracoclaviculare an der Gelenkbildung. Die Tuberositas supraglenoidalis ist kräftig ausgebildet, steht allerdings nicht weit vor.

Die Längsachse des Humeruskopfes ist wiederum schräggestellt. Das Tuberculum majus überragt den Humeruskopf und ist in rostrocaudaler Richtung ausgedehnt, wobei seine Innenseite als konvexer, eiförmiger Gelenkkopf ausgebildet ist. Das Tuberculum minus ist ebenfalls kräftig und weit ausladend; es überragt den Humeruskopf gleichfalls, wenn auch weniger als das Tuberculum majus. Zwischen Caput und den Tubercula liegen tiefe Rinnen, die mit Gelenkknorpel versehen sind. Sie führen in die grubige Vertiefung hinter der Crista pectoralis.

Diskussion

Mit den dargestellten Befunden wird dokumentiert, daß allen Familien der Überfamilie Vespertilionoidea ein sekundäres Schultergelenk zukommt. Hierauf haben andere Autoren bereits zuvor hingewiesen, zumeist allerdings, da der Bau des Schultergelenks nicht ihr primäres Anliegen war, ohne anzumerken, auf welchen Befundgrundlagen ihre Aussagen beruhen. MILLER (1907) und WEBER (1928) schreiben beide korrekterweise allen Vespertilionoiden ein sekundäres Schultergelenk zu, wobei ersterer sogar auf die morphologischen Unterschiede zwischen den Familien eingeht. KOOPMAN (1994) ist in bezug auf die Furipteriden unsicher und schreibt: „Trochiter of humerus making, at most, only a slight articulation with the scapula". Bei den anderen Familien stimmt er mit MILLER (1907) und WEBER (1928) überein.

Vergleicht man den Bau des sekundären Schultergelenks bei den Familien der Vespertilionoidea, ergeben sich zwischen den Familien erhebliche Unterschiede in den morphologischen Details und damit zum Teil auch im Differenzierungsgrad. Nimmt man die Ausdehnung der sekundären Gelenkfläche im Verhältnis zur Cavitas glenoidalis als Maßstab für die Differenzierung, so ist das sekundäre Schultergelenk unter den hier vorgestellten Formen bei *Furipterus* am schwächsten, bei *Myzopoda* und vor allem bei *Mystacina* am weitesten entwickelt, *Natalus* und *Thyroptera* rangieren dazwischen. Die sekundäre Gelenkfläche auf der Dorsalseite der Scapula ist zwar unter dem hier vorgestellten Formen bei den Vertretern der Myzopodidae und Mystacinidae relativ am größten. Sie erreicht aber nicht die Ausdehnung wie bei manchen Vespertilionidae (*Nyctalus*) und Molossidae, bei denen ihre Größe nahezu an die der Cavitas glenoidalis heranreicht. Bei diesen sind auch Tuberculum majus, Tuberositas supraglenoidalis und die Vertiefung hinter der Crista pectoralis auf der Proximalfläche des Humerus sehr viel prägnanter ausge-

bildet. Vespertilionidae und Molossidae unterscheiden sich, soweit bisher untersucht, von den hier vorgestellten Formen weiter durch eine ins Auge fallende Verkleinerung des Tuberculum minus, das gegenüber dem mächtig entwickelten Tuberculum majus den Eindruck erweckt, reduziert zu sein.

Die hier für *Natalus*, *Thyroptera* und *Mystacina* gefundene Einbeziehung eines Lig. coracoclaviculare in das sekundäre Schultergelenk ist zwar, soweit dies anhand des verfügbaren Materials beurteilt werden kann, kein allgemein gültiger Befund für das sekundäre Schultergelenk, aber möglicherweise bei anderen Formen (Schlosser-Sturm und Schliemann 1995) bisher übersehen worden. Durch die sekundäre Gelenkfläche und das Ligament wird, wie geschildert wurde, eine Gelenkoberfläche geschaffen, die dem Ausschnitt aus einer Zylinderinnenwandung ähnelt. In diese Gelenkfläche paßt ein Tuberculum majus – seine dem Caput zugewandte Fläche – von annähernd walzenförmiger Gestalt. Eine ebensolche Oberfläche des Tuberculum majus besitzen auch *Nyctalus* und *Molossus*, so daß es naheliegt, auch bei ihnen ein entsprechend konstruiertes sekundäres Gelenk zu vermuten.

Außer den Familien der Vespertilionoidea verfügen die Vertreter weiterer Familien der Microchiroptera über ein sekundäres Schultergelenk. Und zwar handelt es sich um die Phyllostomidae, Craseonycteridae und Rhinolophidae (Miller 1907; Koopman 1994; Schlosser-Sturm und Schliemann 1995; Weber 1928 u. a.). Für die Beurteilung des Differenzierungsgrades des sekundären Gelenks in den einzelnen Familien läßt sich wiederum die relative Größe der sekundären Gelenkfläche und zusätzlich auch ihre Oberflächengestaltung, die Größe des Tuberculum majus humeri, sowie die Ausprägung der Tuberositas supraglenoidalis und der grubigen Vertiefung auf der Proximalfläche des Humerus heranziehen. In einem solchen Vergleich, der die gesamte Unterordnung umfaßt, weisen die Phyllostomidae das am wenigsten differenzierte sekundäre Schultergelenk auf, die Vespertilionidae und die Molossidae das am weitesten entwickelte, und vor diesen reihen sich die Mystacinidae und Myzopodidae ein.

Weber (1928) weist in seiner tabellarischen Synopse über die Chiropterentaxa und ihre Merkmale denselben Familien, für die jetzt ein sekundäres Schultergelenk gefunden wurde (Schlosser-Sturm und Schliemann 1995 sowie diese Untersuchung), eine solche Sonderbildung zu (selbstverständlich ohne die Craseonycteridae, die noch nicht bekannt waren). Er geht nicht auf morphologische Details und Unterschiede zwischen den Familien ein, bezieht im übrigen aber die Noctilionidae in die Reihe der Familien mit sekundärem Schultergelenk ein: „Tuberculum majus bildet kleines sekundäres Schultergelenk". Dies ist jedoch nicht richtig, denn *Noctilio* gehört mit seinem langgezogenen, proximal fast gratförmigen Humeruskopf nicht zu den Formen mit einer sekundären Gelenkung zwischen Humerus und Scapula, sondern zu der anderen Spezialisationsreihe des Schultergelenks (Schlosser-Sturm und Schliemann 1995). Das Adjektiv „kleines" in der Beschreibung von Weber (1928) mag darauf hinweisen, daß ihm die morphologische Situation nicht eindeutig erschien. In bezug auf die Noctilionidae ist auch Miller (1907) nicht ganz entschieden, wenn er schreibt „Humerus with trochiter much smaller than trochin, its articulation with scapula slight and indefinite, by an ill-defined surface less than one-third as large as glenoid fossa". Unsere Befunde (Schlosser-Sturm und Schliemann 1995), auch unter dem Rasterelektronenmikroskop, haben klar ergeben, daß sich auf der Scapula von *Noctilio* keine zusätzliche Gelenkfläche befindet. Ansonsten gibt es zwischen den kürzlich publizierten Befunden und den hier vorgestellten sowie Millers (1907) kurzen, prägnanten Beschreibungen, die sich allerdings nur auf die Größe des Tuberculum majus und der sekundären Gelenkfläche auf der Scapula beziehen, weitgehende Übereinstimmung, auch hinsichtlich der Beurteilung der Differenzierungsunterschiede zwischen den Familien.

Der Umstand, daß das Schultergelenk der meisten Microchiropteren morphologisch vom Grundbauplan der Säuger abweicht, macht es erforderlich, nach den funktionellen

Gegebenheiten zu fragen, unter denen diese Abweichungen entstanden sind. Eingangs wurde bereits darauf hingewiesen, daß das sekundäre Schultergelenk nur eine dieser Abweichungen darstellt. Die andere mit ihrem mehr oder weniger ovoid gestalteten Caput humeri und einer entsprechend gebauten Cavitas glenoidalis ist ebenfalls weit verbreitet und kommt, soweit dies aus dem bisher untersuchten Material geschlossen werden kann (Schlosser-Sturm und Schliemann 1995), bei Noctilionidae, Mormoopidae, Emballonuridae und Megadermatidae vor.

Das sekundäre Gelenk mit seinen zusätzlichen Gelenkflächen ist aus morphologischer Sicht die aufwendigere der beiden Konstruktionen. Ihr wurde von Vaughan (1959) und nachfolgend von verschiedenen anderen Autoren (u. a. Altenbach 1979; Norberg 1970; Smith 1972; Strickler 1978) die Funktion zugeschrieben, den Flügelaufschlag am oberen Umkehrpunkt zu begrenzen. Diese funktionelle Vorstellung wurde kürzlich ausführlich erörtert und abgelehnt (Schlosser-Sturm und Schliemann 1995), nachdem zuvor schon einmal durch Schlosser-Sturm (1982) eine von Vaughans (1959) Vorstellungen abweichende Funktion diskutiert worden war. Es wurde jetzt (Schlosser-Sturm und Schliemann 1995) versucht, mit einem umfassenderen Ansatz, der flugbiologische Gesichtspunkte und auch myologische Befunde mit einbezog, für beide morphologische Abwandlungen des Schultergelenks eine einheitliche funktionelle Erklärung zu finden. Dies führte zu der Hypothese, daß beide Konstruktionen während des Flügelabschlages die Drehbarkeit des Humerus im Schultergelenk im Sinne einer Innenrotation einschränken. In eben dieser Weise wirken jedoch Abschlagmuskulatur und der Luftdruck unter dem Flügel, der an seinem vorderen Rand vom Skelettapparat gestützt wird. Einwärtsrotierend wirkende Kräfte sind für eine mehr oder weniger horizontale Flugposition des Rumpfes erforderlich und werden daher vom Bewegungsapparat auf den Rumpf übertragen, aber sie dürfen nicht zu unphysiologischen Drehbewegungen des Humerus gegenüber dem Rumpf führen. Das funktionelle Erfordernis der Einschränkung von Rotationsbewegungen gilt für alle Chiropteren, und es erklärt, warum sich bauliche Veränderungen des Schultergelenks vielfach entwickelt haben. Mit ihrer Hilfe, also mit Einrichtungen des passiven Bewegungsapparates, lassen sich Drehbewegungen im Schultergelenk ökonomischer als durch Muskelkraft einschränken. Hierauf gibt es auch Hinweise, die sich aus Befunden vergleichend myologischer Art ergeben (Schlosser-Sturm und Schliemann 1995).

Die Taxa der Vespertilionoidea sind, wie oben erwähnt, in der Konstruktion ihres Schultergelenks ausschließlich den Weg der Entwicklung zu einem sekundären Schultergelenks gegangen. Ob dieser Gelenktyp bei ihnen, wie dies für die Microchiroptera insgesamt zutrifft, mehrmals unabhängig entstanden ist, muß offen bleiben.

Danksagung

Herrn Prof. Dr. Gerhard Storch, Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt, danke ich für die freundliche Überlassung des Materials von *Natalus*, *Furipterus* und *Mystacina* und Frau E. Frerichs, Zoologisches Institut und Zoologisches Museum, Hamburg, für die Anfertigung der Zeichnungen.

Zusammenfassung

Das Schultergelenk der Microchiropteren erfährt in fast allen Familien morphologische Veränderungen. Entweder wird der halbkugelige Humeruskopf in Richtung auf eine mehr oder weniger langgestreckt eiförmige Gestalt bei korrespondierender Veränderung der Cavitas glenoidalis der Scapula abgewandelt, oder das vergrößerte Tuberculum majus artikuliert in einem sekundären Schultergelenk mit einer zusätzlichen Gelenkfläche auf der Dorsalseite der Scapula. Aus der umfangreichen Super-

familie Vespertilionoidea ist bisher nur das sekundäre Schultergelenk bekannt geworden. In diesem Zusammenhang liegen Befunde aus den Familien Vespertilionidae und Molossidae vor. Gut dokumentierte Untersuchungen von Vertretern der übrigen Familien der Vespertilionoidea standen bisher noch aus. So ist auch verständlich, daß entsprechende Hinweise in der Literatur nicht immer hinlänglich klar waren. Für die vorliegende Studie wurde das Schultergelenk von Mitgliedern der Familien Natalidae, Furipteridae, Thyropteridae, Myzopodidae und Mystacinidae untersucht. Hierbei zeigte sich, daß auch diese Familien der Vespertilionoidea durch ein sekundäres Schultergelenk ausgezeichnet sind. Damit ist einerseits dokumentiert, daß in dieser Überfamilie als morphologische Veränderung des Schultergelenks nur das sekundäre Gelenk realisiert wurde. Andererseits zeigte sich, daß dieses sekundäre Gelenk in den einzelnen Familien sehr unterschiedlich weit differenziert ist. Als ein Gradmesser für das Ausmaß der Differenzierung muß unter anderem die relative Größe der sekundären Gelenkfläche des Schulterblattes gelten. Danach besitzt *Furipterus* das am schwächsten entwickelte sekundäre Schultergelenk, *Myzopoda* und *Mystacina* die am weitesten differenzierten. *Natalus* und *Thyroptera* nehmen eine Position dazwischen ein. Das Gelenk erreicht allerdings bei keinem der hier vorgestellten Taxa den Ausbildungsgrad wie bei den bisher untersuchten Vespertilionidae (*Pipistrellus*, *Nyctalus*) und Molossidae. Beiden morphologischen Abwandlungen des Schultergelenks wird die Funktion zugedacht, während des Abschlages des Flügels die Drehbarkeit des Humerus in der Cavitas glenoidalis und gegenüber dem Rumpf einzuschränken. Und beide Veränderungen sind bei den Microchiroptera mehrfach und unabhängig voneinander in paralleler Evolution entstanden.

Literatur

Altenbach, J. S. (1979): Locomotor Morphology of the Vampire Bat, *Desmodus rotundus*. Spec. Publ. Amer. Soc. Mamm. **6**, 1–137.

Koopman, K. F. (1994): Chiroptera: Systematics. In: Handbuch der Zoologie. Ed. by J. Niethammer, H. Schliemann und D. Starck. Berlin, New York: Walter de Gruyter. Vol. **8**.

Miller, G. S. (1907): The Families and Genera of Bats. Washington: Government Printing Office.

Norberg, U. M. (1970): Functional osteology and myology of the wing of *Plecotus auritus* Linnaeus. (Chiroptera). Ark. Zoo. **22**, 483–543.

Schlosser-Sturm, E. (1982): Zur Funktion und Bedeutung des sekundären Schultergelenks der Microchiropteren. Z. Säugetierkunde **47**, 253–255.

Schlosser-Sturm, E.; Schliemann, H. (1995): Morphology and function of the shoulder joint of bats (Mammalia: Chiroptera). J. Zool. Syst. Evol. Res. **33**, 88–98.

Smith, J. D. (1972): Systematics of the Chiropteran Family Mormoopidae. University of Kansas, Museum of Natural History, Misc. Publication **56**, 1–132.

Strickler, T. L. (1978): Functional osteology and myology of the shoulder in the Chiroptera. Basel, New York: Karger Verlag.

Vaughan, T. A. (1959): Functional morphology of three bats: *Eumops*, *Myotis*, *Macrotus*. Publ. Univ. Kansas Mus. Nat. Hist. **12**, 1–153.

Weber, M. (1928): Die Säugetiere. Jena: Gustav Fischer.

Anschrift des Verf.: Prof. Dr. Harald Schliemann, Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg

Z. Säugetierkunde **62** (1997) 330–338

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Leopard-cats, *Prionailurus bengalensis* (Carnivora: Felidae) from Indonesia and the Philippines, with the description of two new subspecies

By C. P. Groves

Department of Archaeology and Anthropology, Australian National University, Canberra, Australia

Receipt of Ms. 03. 01. 1997
Acceptance of Ms. 18. 03. 1997

Abstract

Studied was the geographic variation of leopard-cats (*Prionailurus bengalensis*) in Malaysia, Indonesia and the Philippines. Distinct subspecies can be recognised for: Java and Bali; Sumatra; Borneo; Palawan; and Negros. These show unexpected zoogeographic patterns. On the Malay peninsula a probable hybrid population exists.

Introduction

The leopard-cat, *Prionailurus bengalensis* Kerr, 1792, is one of the most widespread species of the family Felidae, from South Asia through East Asia to the Russian Far East, and Southeast Asia to western Indonesia, and the Philippines (Nowell and Jackson 1996).

The Malay/Indonesian distribution covers the Malay Peninsula, Sumatra, Borneo, Java, Bali, and offshore islands. Geographic variation in Indonesia has been treated by Brongersma (1935) and Sody (1949). Brongersma (1935) recognised the following subspecies:

P. b. sumatranus (Horsfield, 1821). Sumatra and P. Tebingtinggi; *P. b. javanensis* (Desmarest, 1816). Java and Bali: *P. b. borneoensis* Brongersma, 1935. Borneo.

Sody (1949) recognised these same subspecies, in addition keeping his options open whether the form from P. Tebingtinggi might not also represent a separate subspecies, *P. b. tingia* (Lyon, 1908).

In the Philippines the species is found in Palawan, Calamianes, Panay, Negros, and Cebu. There has never been a comparison of Philippines leopard-cats with those from any other area. Sanborn (1952) recorded several specimens from Palawan and one from Negros, remarking on the variability within Palawan ("two colour phases, a dark gray and a dull brown"), and noting that the Negros skin was "bright red-brown" and "much larger than any from Palawan". Rabor (1977), who called the species *Felis minuta* Temminck, said only that specimens from Negros "possess brighter colors than those from Palawan".

The aim of this study is to review the species in Indonesia, and to provide for the first time a comparative description of Philippines leopard-cats.

Material and methods

147 skins and 100 skulls of Southeast Asian leopard-cats have been studied in the following collections: Museum Zoologici Bogoriense, Bogor, Indonesia (MZB); Zoological Reference Collection, Singapore (ZRCS); Sarawak Museum, Kuching, Malaysia (SMK); Rijksmuseum van Natuurlijke Historie, Leiden, Netherlands (RML); Instituut voor Taxonomisch Zoologie, Amsterdam, Netherlands (ZMA); Natural History Museum, London, U.K. (BMNH); Field Museum, Chicago, U.S.A. (FMNH).
The skins were compared visually. The following craniodental measurements were taken: Greatest Skull Length; Condylobasal Length; Bizygomatic Breadth; Postorbital Constriction Width; Interorbital Breadth; Bicanine Breadth; Mandible Length; Upper Carnassial (P^4) Length; Lower Carnassial (M_1) Length. The skull measurements were subjected to Discriminant Analysis using SPSS for Windows (site-licensed to the Faculty of Arts, Australian National University).

Results

Pelage

Compared to leopard-cats from India, Burma and the Indochinese region (here treated as nominotypical *P. b. bengalensis*), those from insular/peninsular Southeast Asia (the Sundaic subregion) have a darker ground colour, especially along the median dorsal zone; smaller spots (which are rarely rosette like); and narrower longitudinal stripes on the nape and withers. Skins from Bangkok, Mergui and Tenasserim (including the type of *Felis tenasserimensis* Gray, 1867) resemble more northerly Burmese and Indochinese skins: off-white ground colour, with larger, more rosette-like spots and broader longitudinal stripes.

Within the Sundaic subregion, there are two strikingly different colour groups:

1) Light grey, with very small spots which are often not very clearly expressed. The three spot-lines along the middle of the back do not form complete stripes, and are thin and close together. Java, Bali, and Palawan.
(a) In Java and Bali the grey is pale, often yellow-grey; the two pairs of longitudinal nape-stripes are of equal width, or the outer pair may be slightly broader.
(b) In Palawan the grey is more ochery-toned; the relation between the nape-stripes is as in Borneo.

2) Warm ochery toned, with larger, clear black spots. The three longitudinal spot-lines are usually fused into complete stripes, or nearly so, and thicker, less close together than in Java or Palawan. Sumatra, Borneo and Negros.
(a) In Borneo, the inner pair of nape-stripes is always thinner than the outer, usually markedly so. Occasional individuals are slightly greyer than usual, but do not resemble Javan skins.
(b) In Sumatra, the nape-stripes are of approximately equal width. The colour averages less bright than in Borneo, and the spots are somewhat smaller.
(c) Negros skins resemble those from Borneo, but are darker.

This neat geographic division is spoiled to some degree by skins from the Malay peninsula, which are variable in colour: of the skins in London and Singapore, two are grey like those from Java, four are ochery like Sumatra, and 15 are light fawn like Indo-Burmese skins, while the spots in six of the latter tend towards rosette form. The spots, even if small like those of insular forms, are always "shaded" like other mainland leopard-cats: that is, each spot is lighter (light brown) anteriorly and darker (blacker or dark brown) posteriorly. The nape-stripes are of equal width; the spot-rows are narrow, less formed, more broken up than in insular specimens.

Table 1. Measurements of *P. bengalensis*

	Negros	Palawan	Mainland	Sumatra	Java	Borneo	Bali
			Males				
Greatest skull length							
Mean	88.4	85.2	95.0	89.9	87.5	86.8	83.5
s. d.	1.57	0.97	3.00	3.08	2.95	2.45	2.65
Range	87.0–90.1	84.0–86.7	92.0–98.0	87.0–93.0	86.0–94.0	83.0–90.0	81.0–87.0
n	3	5	3	7	12	8	4
Condylobasal length							
Mean	83.3	77.7	84.0	80.4	80.8	79.4	78.0
s. d.	–	0.68	2.65	3.55	3.77	2.20	2.58
Range	82.0–84.6	77.0–78.4	80.0–85.0	75.0–83.0	77.0–83.0	77.0–82.0	75.0–81.0
n	2	5	3	7	12	8	4
Bizygomatic breadth							
Mean	57.5	54.4	63.7	59.7	56.2	58.3	52.0
s. d.	2.45	2.21	2.08	3.50	2.78	1.44	2.00
Range	55.0–59.9	52.4–58.0	61.0–63.0	55.0–64.0	54.0–60.0	56.0–61.0	50.0–57.0
n	3	5	3	7	12	8	4
			Females				
Greatest skull length							
Mean	82.1	79.8	89.7	87.0	82.9	85.1	–
s. d.	–	–	2.73	2.16	3.55	2.97	–
Range	81.1–83.0	–	85.0–92.0	85.0–90.0	76.0–88.0	84.0–88.0	–
n	2	1	6	4	9	7	–
Condylobasal length							
Mean	77.8	72.5	81.8	78.3	72.8	77.1	–
s. d.	–	–	1.60	2.63	4.15	2.69	–
Range	76.5–78.0	–	79.0–82.0	76.0–82.0	66.0–80.0	74.0–82.0	–
n	2	1	6	4	9	6	–
Bizygomatic breadth							
Mean	53.6	49.1	60.2	56.9	51.9	56.6	–
s. d.	–	–	0.75	2.72	2.88	2.97	–
Range	53.2–54.0	–	59.0–61.0	54.0–64.0	49.0–58.0	55.0–62.5	–
n	2	1	6	4	9	8	–
			Sexes combined				
P^4 length							
Mean	10.0	9.4	9.9	9.8	9.5	9.8	–
s. d.	0.17	0.31	0.35	0.41	0.47	0.71	–
Range	9.9–10.2	9.0–9.9	9.0–10.0	9.0–10.0	9.0–10.0	9.0–11.0	–
n	4	6	8	6	11	8	–
Tail as percent of Head + Body length							
Mean	43.5	48.8	50.1	40.4	46.0	47.0	–
s. d.	–	7.54	5.21	4.43	4.29	4.92	–
Range	–	44–60	44–56	36–47	37–55	40–55	–
n	1	4	7	4	22	11	–

Tail length

Tails are shorter in insular leopard-cats than in those from the mainland, and vary among themselves (Tab. 1). The tail is especially short in the Sumatran and Negros forms, longer in the others; in the Palawan form, it is nearly as long as in those from the mainland.

Skulls and teeth

Skull size of males decreases in the sequence Mainland–Sumatra–Negros–Java–Borneo–Bali–Palawan, with overlaps between the ranges of all but the smallest and largest taxa (Tab. 1). In females the sequence is different, so that sexual size difference, as indicated by mean condylobasal length in female as a percentage of that in male, is much more in Java (90.1%) and Palawan (93.3% – but only one female skull available) than in other populations (97.1–97.4% in Mainland, Sumatra and Borneo, 98.6% in Negros).

The skull is narrower in Java and Palawan than in other populations. The two Philippine forms have much less development of cranial crests, so that Greatest Skull Length (prosthion to opisthocranion) is comparatively less compared to condylobasal length than in the Indonesian and mainland forms; this is especially marked in Negros.

The carnassials (represented in table 1 by P^4, for which larger samples are available than for M_1) average smaller in Java and Palawan than in other populations.

Discriminant Analysis using all adult and late-juvenile crania (Fig. 1) separates four groups: Negros, Palawan, Java, and Sumatra/Borneo/Mainland. Palawan is intermediate between Negros and the two other clusters. Function 1, on the abscissa, accounts for 48.3% of the total variance; it does not correlate strongly with any of the original variables, but weakly contrasts mandible length, condylobasal length and interorbital breadth with postorbital breadth. Function 2, along the ordinate, accounts for 29.1% of the variance; it is largely a size function, emphasising breadth measures more than length. Restricting the analysis to adults only reduced the dataset too much to achieve meaningful results.

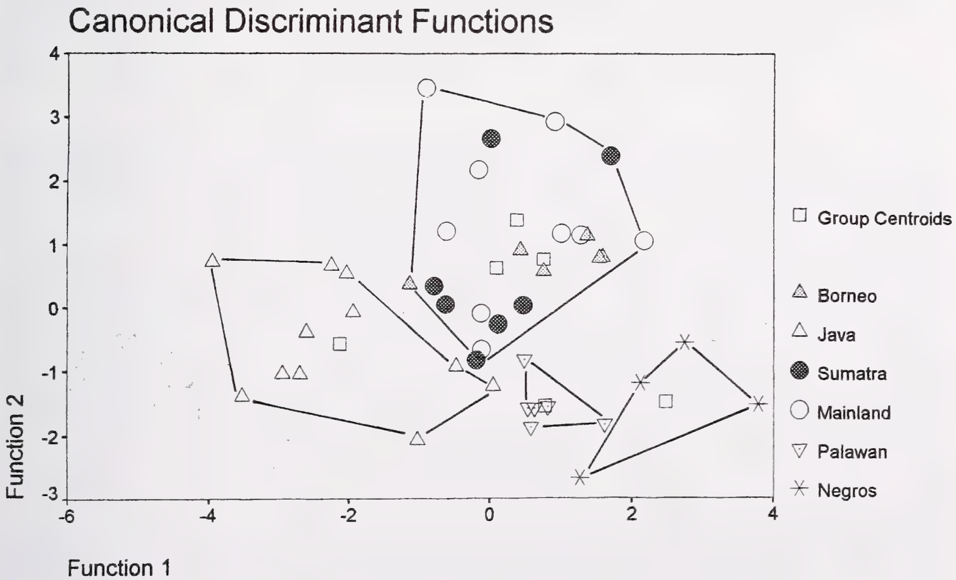


Fig. 1. Plot of First and Second Discriminant Functions for skull and tooth measurements of Southeast Asian leopard cats (*Prionailurus bengalensis*).

Thus, the insular leopard-cats divide into two phenetic groups on several characters: colour and pattern, sexual dimorphism, skull shape, and upper carnassial size. In Java and Palawan colour is greyer, the spotted pattern is less marked, male-female size difference is more marked, skulls are narrower, and P^4 is shorter. In Sumatra, Borneo and Negros colour is more ochery, spots are blacker, there is less size difference between the sexes, skulls are broader, and the upper carnassial is longer. The total-evidence approach to cranial morphology, however, shows that the Negros cranium is the most distinctive, and the Palawan form is intermediate between Negros and the two different (Java, Sumatra-Borneo-Mainland) western Sundaland forms.

Discussion

The relationships of each of the insular forms now need to be discussed.

(a) Philippines. There is an interesting zoogeographical problem. Heaney (1985, 1986) has surveyed the zoogeographic affinities of the Philippines; only in the case of Palawan is there evidence for a former land-bridge to Sundaland (= the shallow-water islands of western Indonesia), and Palawan does possess a distinctly Sundaic mammalian fauna, whereas Mindanao and Luzon show high endemicity. The fauna of Negros is very poorly known; only 13 mammal species other than bats are recorded. On this admittedly limited evidence, faunal similarity indices cluster Negros with the Philippine (non-Palawan) Faunal Province, specifically with Luzon and Mindoro.

On the other hand there is emerging evidence that Negros, together with Cebu and Panay which lie on the same shallow-water shelf, does have its own endemic suite of species, including a deer (*Cervus alfredi*), a pig (*Sus cebifrons*), a shrew (*Crocidura negrina*) and a cloud-rat (*Crateromys heaneyi*). But none of these species, unlike the leopard-cat, has a direct Sundaland affinity; rather, they are all either vicariants of Luzon-Mindanao taxa, or else primitive relicts which have presumably been replaced elsewhere in the Philippines by later invaders from outside the region. The leopard-cat in Negros appears to be unique in having no conspecifics (no close competitors) in the Luzon and Mindanao faunal regions; either the species once inhabited these other islands and has gone extinct there, or else it has dispersed directly, overwater, from Palawan or from Borneo (via the Sulu chain?). The cranial evidence suggests that Palawan is the source; the pelage data would favour Borneo.

(b) Borneo and Sumatra. Consistent, if minor, differences exist between the Bornean and Sumatran leopard-cats. They appear to be correctly assigned to distinct subspecies.

(c) Bali. Limited evidence suggests that the leopard-cat of Bali differs on average only from that of Java. Subspecific distinction is probably not warranted.

(d) Mainland. The leopard-cat of the Malay peninsular is closely similar to that of the Indo-Chinese region. This differs from most mammals: a Malay-Sumatran affinity is more usual (reviewed by Lekagul and McNeely 1977). A few facts, such as the occurrence in the Malay peninsula of individuals with a more Sumatran-like colouring, suggest the former presence of a common Sundaic form there, since swamped by gene-flow from the north. Despite average differences, it is not possible to distinguish the peninsular leopard-cat from the common mainland Southeast Asian one; whether this in turn is distinct from the Indian subspecies, nominotypical *bengalensis*, is outside the scope of this study. The "Mainland" sample of leopard-cat studied for comparative purposes for this study will be designated simply "cf. *bengalensis*".

(e) Java. The grey, rather pale-spotted pelage of the Java population is duplicated only in Palawan; nowhere else in the entire range of the species does a comparable morph occur. On the other hand it is not dissimilar to the pelage of congeneric *Prionailurus rubiginosus* and *P. viverrinus* (though in the latter the markings are more nearly

black). The difference between the grey and ochery morphs could actually be genetically very simple; the grey morph in some respects recalls the chinchilla mutation at the C locus which reduces yellow pigmentation and occurs in several species of felids (Robinson 1978); the difference in the present instance would be that it has become fixed (independently?) in two different *P. bengalensis* populations, and in two entire species of the same genus. This hypothesis proposes that a chinchilla mutation is at the base of these pelage features, not that it is responsible for them in their entirety.

In conclusion, the following subspecies may be recognised in the insular and peninsular Southeast Asian region (Malaysia, Indonesia, Philippines):

Prionailurus bengalensis javanensis (Desmarest, 1816)

Distribution: Java and Bali.

Specimens seen: Skins: Java: BMNH 27; ZRCS 1; MZB 26; Bali; BMNH 5. Skulls: Java: MZB 11; BMNH 6; RML 8; Bali: BMNH 4.

Diagnosis: Grey with very small, longitudinally elongated, poorly expressed spots; nape-stripes of equal width, or outer pair slightly broader; median dorsal spot-lines very close together. White midfacial streak extends from forehead to muzzle; white cheek zone not clearly demarcated with black stripes; throat collars poorly marked. Tail length averaging 46% of head plus body; tail spots especially vaguely marked. Skull length in males equivalent to other Indonesian subspecies, but that of females much smaller, hence unusually sexually dimorphic (female condylobasal length only 90% that of male); skull relatively narrow; upper carnassial averaging shorter than other Indonesian forms.

Notes: Colour in Java is light grey or grey-yellow with just a hint of tawny, occasionally with pinky-ochery tones. The spots tend to be reddish-toned. Balinese specimens are even greyer, spots even less distinct, than the average from Java, though not outside the Java range; male skull averaging smaller, but ranges and standard deviation limits overlap.

Prionailurus bengalensis sumatranus Horsfield, 1821

Distribution: Sumatra, including the offshore island of Tebingtinggi.

Specimens seen: Skins: BMNH 4, including the type of *sumatrana*; ZRCS 2; MZB 8. Skulls: MZB 3; ZRCS 3; RML 2; ZMA 3.

Diagnosis: Less bright ochery than *borneoensis*, with smaller spots; nape stripes of approximately equal width; dorsal spot-rows close together, tend to coalesce into continuous but thin longitudinal stripes. Tail short, averaging 40.4% of head plus body. Underparts creamy-white; well-spotted on chest, upper belly, and inner aspect of hindlegs; inner surface of forelegs less well-spotted, but always two dark bands across humerus. White mid-facial streak extends well onto muzzle. Dark cheek stripes, demarcating white zone of cheeks above and below, very thick; lower stripes turn medially and form a collar across upper throat, with a second collar behind this. Skull broader than *javanensis*; less sexually dimorphic (female condylobasal length 97.4% of male; upper carnassial averaging longer.

Notes: Brongersma (1935) regarded *Felis tingia* Lyon, 1908, from P. Tebingtinggi, as a probable synonym of *sumatranus*. At the same time he described a skull and "several" skins (the latter from photographs) from Nias, considering it possible that they could represent a separate subspecies; since that date, however, no further evidence of this putative taxon has become available.

Prionailurus bengalensis borneoensis Brongersma, 1935

Distribution: Borneo.

Specimens seen: Skins: BMNH 11; ZRCS 1; SMK 21; MZB 3. Skulls: MZB 2; ZRCS 6; SMK 16; RML 1; BMNH 7.

Diagnosis: Rich ochery colour, darkened in middorsal region, with comparatively large, clearly marked black spots; inner pair of nape-stripes always thinner than outer, usually markedly so; median dorsal spot-lines joined into stripes, completely or nearly so. Underparts, throat, facial markings similar to *sumatrana.* Tail averaging 47% of head plus body. Skull as *sumatrana*, but slightly smaller.

Notes: Two skins in the Sarawak Museum are noticeably greyer than any other, and a few others tend towards a greyish tone; but colour is never as grey as in *javanensis*, and the spots are larger and blacker than the latter.

Brongersma (1935) discussed the name *Felis undata* Desmarest, often previously used for this subspecies. He concluded that, the type being lost and the description well-nigh indeterminable (it may even refer to a feral domestic cat), this name cannot be used for any taxon of leopard-cat.

Prionailurus bengalensis cf. *bengalensis* (Kerr, 1792)

Distribution: Mainland Southeast Asia, from the Malay peninsula north at least into Burma and the Indochinese peninsula.

Specimens seen: Skins: BMNH 9; ZRCS 12. Skulls: ZRCS 9; BMNH 3.

Localities: Specimens examined for this study are from Serembang, Negri Sembilan; Tebing Tingii, Kelantan (N. B. this is not P. Tebingtinggi in Sumatra); Johore; K. Kangsar, Perak; Melaka; Selitar.

Diagnosis: Colour usually light fawn, even creamy-toned, on flanks, somewhat contrasting with tawny tone in mid-dorsal region; spots often comparatively large, though rarely as large as bengalensis, but always of "shaded" type; nape-stripes of equal width or the inner pair somewhat thinner than the outer; dorsal spot-rows narrow, ill-formed, tend to be broken up. Tail length about half that of head and body. Skull larger than insular subspecies, and not very sexually dimorphic (female condylobasal length 97.4% of male).

Notes: Colour is more variable than in the insular forms; it is usually as above, but occasional specimens are grey as *javanensis* or ochery as *sumatrana.* As is common in Indochinese populations of *bengalensis*, both large-spotted and small-spotted forms occur, though the spots are rarely as large or rosette-like as in Indochina, while the stripes are less broad and the colour is less pale. The spots in the small-spotted type resemble *sumatrana* except that they are "shaded" like the large-spotted type: that is, they are light brown anteriorly, becoming dark brown posteriorly.

As suggested above, the most plausible interpretation of this variability would seem to be that gene-flow from further north in Southeast Asia has overwhelmed, but not yet entirely submerged, a population formerly of Sundaic affinity.

Prionailurus bengalensis rabori new subspecies

Type: FMNH 74326, adult female, skin and skull, from Canlaon, Negros Oriental. Collected by D. S. Rabor, 24th April 1953.

Distribution: Negros; presumably also Cebu and Panay, whence the species has been recorded.

Specimens seen: Skins: BMNH 2; FMNH 5. Skulls: BMNH 2; FMNH 9.

Diagnosis: Dark ochery to buffy fawn in colour, less bright than *borneoensis* especially in median dorsal region; spots large (but smaller than *borneoensis*), dark; median dorsal spot-rows forming nearly continuous stripes; median nuchal stripes very broad, median pair much narrower than lateral pair, failing to reach shoulders. A single black collar between interramal area and throat (posterior collar missing). White face streak short, does not extend far onto muzzle. Tail more clubby than other insular forms; its length (in a single specimen, the type) 43.5% of head and body. Skull of male averaging larger than Indonesian forms, of female equivalent in size to *sumatrana* and *borneoensis*, but poorly crested in both sexes so that Greatest Length is low compared to Condylobasal Length; skull somewhat narrower than latter two, but not as narrow as *javanensis*. Upper carnassial averaging longer than other insular forms. Measurements of type (in mm): Greatest Skull Length 81.1, Condylobasal Length 76.5, Bizygomatic Breadth 53.2, Postorbital Constriction 23.9, Interorbitat Breadth 14.0, Bicanine Breadth 19.6, Mandible Length 52.8, P^4 length 10.2, M_1 length 6.9; Total Length 396, Tail 120, Hindfoot 15, Ear 17.

Notes: Sanborn (1952) and Rabor (1977) called Philippine leopard-cats *Felis minuta* Temminck, 1825, noting but not formalising differences between cats from Negros and Palawan. As correctly recorded by Brongersma (1935), the syntypes of this species (in the Leiden Museum) are from Java and are examples of *P. b. javanensis*.

Etymology: for the late Dioscoro S. Rabor, doyen of the Filipino mammalogy (and ornithology) community. Professor Rabor died in 1995, after a long illness. His long and active career has inspired a flourishing school of faunal studies and conservation action in the Philippines, and spawned a new generation of wildlife enthusiasts.

***Prionailurus bengalensis heaneyi* new subspecies**

Type: FMNH 62896, nearly-adult male (with spheno-occipital synchondrosis not fully fused), skin, skull and skeleton, from Puerto Princesa, Palawan. Collected by H. Hoogstraal, May 5th, 1947.

Specimens seen: Skins: BMNH 1; FMNH 9. Skulls: BMNH 2; FMNH 3.

Diagnosis: Colour grey-fawn with small, dark brown spots on flanks; inner pair of nape-stripes always thinner than outer, both pairs reaching back to scapular level; dorsal spot-lines usually incomplete, close together, thin. White midfacial streak long, reaching muzzle. Tail long, averaging 48.8% of head and body; only vaguely spotted. Skull small in male, and even more so in female; condylobasal length of single available female only 93.% of male average; skull even narrower than in *javanensis*, though fairly broad across muzzle. Upper carnassial smaller than any other insular subspecies.

Measurement of type (in mm): Greatest Skull Length 85.1, Condylobasal Length 78.4, Bizygomatic Breadth 52.4, Postorbital Constriction 22.1, Interorbital Breadth 12.7, Bicanine Breadth 21.5, Mandible Length 55.0, P^4 length 9.6, M_1 length 7.3.

Notes: Both Sanborn (1952) and Rabor (1977) noted that there is a difference in colour between Palawan and Negros cats, but neither made a taxonomic distinction, presumably having insufficient material.

Etymology: For Larry R. Heaney, leading expatriate connoisseur of the Philippine mammal fauna.

Acknowledgements

I am grateful to the curators of the collections in which *P. bengalensis* were studied: in the MZB, *Bp. Boeadi*; in the ZRCS, Dr. C. M. Yang; in the SMK, Dr. L. Chin; in the RML, Dr. C. Smeenk; in the ZMA, Dr. P. J. H. van Bree; in the BMNH, the late Mr. J. E. Hill and Ms. P. D. Jenkins; and in the FMNH, Dr. L. R. Heaney. I would especially like to acknowledge useful discussions, in person and in correspondance, on Philippine mammals and their zoogeography, with Dr. Larry Heaney.

Zusammenfassung

Die Bengalkatzen (Prionailurus bengalensis) Indonesien und den Philippinen, mit Beschreibung zweier neuer Unterarten.

Die Bengalkatzen (*Prionailurus bengalensis*) Südostasiens zeigen ein unerwartet komplexes biogeographisches Muster. Zwei neue Unterarten werden von den Philippinen beschrieben; die Populationen von der Malayischen Halbinsel sind sehr variabel und könnten das Resultat einer Hybridisierung zwischen sundaischen und Festlandindividuen sein.

Literature

Brongersma, L. D. (1935): Notes on some recent and fossil cats, chiefly from the Malay Archipelago. Zool. Mededel., (Leiden) **18**, 1–89.

Heaney, L. R. (1985): Zoogeographic evidence for Middle and Late Pleistocene lands bridges to the Philippine Islands. Modern Quat. Res. in SE Asia **9**, 127–143.

Heaney, L. R. (1986): Biogeography of mammals in SE Asia: estimates of rates of colonization, extinction and speciation. Biol. J. Linnaean Soc. (London) **28**, 127–165.

Lekagul, B.; McNeely, J. (1977): Mammals of Thailand. Bangkok: Kuruspha.

Nowell, K.; Jackson, P. (1996): Wild Cats: Status Survey and Conservation Action Plan. IUCN/SSC Cat Specialist Group, Cambridge, U. K.: IUCN Publ.

Rabor, D. S. (1977): Philippine Birds and Mammals. Quezon City: Univ. Philippines Press.

Robinson, R. (1978): Homologous coat color variation in *Felis*. Carnivore **1**, 68–71.

Sanborn, C. C. (1952): Philippine Zoological Expedition 1946–47. Fieldiana: Zoology **33**, 89–158.

Sody, H. J. V. (1949): Notes on some Primates, Carnivora, and the *Babirusa* from the Indo-Malayan and Indo-Australian regions. Treubia **20**, 121–190.

Author's address: Colin P. Groves, Department of Archaeology and Anthropology, Australian National University, Canberra, A. C. T. 0200, Australia

Z. Säugetierkunde **62** (1997) 339–349

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Genetic variability of Roe deer populations (*Capreolus capreolus* L.) from northeast Yugoslavia

By Svetlana Milošević-Zlatanović, Jelka Crnobrnja-Isailović, I. R. Savić, and S. Stamenković

Institute of Biology, Faculty of Science, University of Kragujevac, Kragujevac, Institute for Biological Research "Siniša Stanković", Belgrade, and Institute of Zoology, Faculty of Biology, University of Belgrade, Belgrade

Receipt of Ms. 09. 05. 1996
Acceptance of Ms. 26. 09. 1996

Abstract

Tissue samples of 94 roe deer (*Capreolus capreolus* L.) from five populations in Yugoslavia were examined for genetic variability and differentiation at 33 presumptive structural loci by means of horizontal starch gel electrophoresis. The proportion of polymorphic loci varied between 3.3% and 12.1 %. Average heterozygosity per locus varied between 0.2% and 2%. Estimates of standardized variance of gene frequencies (F_{ST}) varied between 0.015 and 0.204 with a mean of 0.110. Indirect estimates of gene flow among populations based on the degree of population subdivision, F_{ST}, was 2.70 migrants per generation, whereas the "private alleles method" showed a gene flow level of 12.26 migrants per generation. Significant heterogeneity of gene frequencies existed between the highland populations south of the Danube. The data on polymorphism, heterozygosity, and gene flow rates are within the range of those reported by other researchers for Hungarian and Bulgarian populations.

An overall assessment of the factors determining the genetic structure of the analysed populations in this part of the roe deer range reveals no evidence of genetic drift, implying that selection or non-random mating are more important determining factors. Our data, together with that in the literature, suggest the existence of a clinal North-South gradient in basic population genetic parameters.

Introduction

In recent years the study of genetic variability of roe deer populations from central and southeastern Europe has been extensively reported by Hartl and Reimoser (1988) and Hartl et al. (1991, 1993). With the exception of one population from Slovenia (Hartl et al. 1993) and three from Central Serbia (Milošević-Zlatanović et al. 1994), the whole range of the roe deer in the former Yugoslavia is poorly represented.

In an attempt to contribute to the knowledge of genetic structure and variability in this part of the species range, we present in this study the results of our analysis of genetic variability in five populations of roe deer from northeast Yugoslavia – three from the lowland area north of the Danube, two from the mountainous region south of the Danube (Fig. 1). Our data are relevant to several hypotheses concerning roe deer population structure: the extent of genetic differentiation within the species range; the possibility of subspecies differentiation, including the proposed existence of north-south clinal variation and the existence and strength of population barriers (Hartl et al. 1991); the existence

and magnitude of ecotypic differentiation within the species (HARTL et al. 1993), and the impact of game management techniques on genetic structure (RYMAN et al. 1980).

Fig. 1. Sampling sites and localities for the five roe deer populations from Yugoslavia. The insert depicts the Kozara enclosure. (1) Bački Monoštor; (2) Kozara; (3) Zrenjanin; (4) Severni Kučaj; (5) Negotin.

Material and methods

A detailed exposition of sampling areas and localities is presented in this first account.

Samples were taken from several localities (Fig. 1), within five hunting areas defined by game management plans. The "Bački Monoštor" area is situated on the left bank of the Danube, from the Hungarian border to the 1407th km of the Danube (45°42′ N, 45°56′ E) on an area of 11,764 hectares. It lies completely within the alluvial plain of the Danube on alluvial pararendzinas and sandy chernozem soils, and is completely fenced. The area is predominantly forested (>50%), with a typical turnover of floodplain forests (ass. *Salicetum albae – Ulmeto-fraxinetum quercetosum – Populetum albae et nigrae – Quercetum roboris*). Grasslands (30%) are represented by pastures (20%) and meadows (10%). The remainder are ecotonal semiwooded habitats. The area is predominantly a red deer reserve with a planned red deer density of 12 individuals per 100 ha. Roe deer are present in an estimated density of 2.3 ind. per 100 ha. A total of 30 roe deer was sampled from the area. To facilitate management, the area is divided arbitrarily into 8 districts. One of these, "Kozara", was separately analysed (15 individuals). It is an area of 900 ha of pastures on solonec soils. It has an estimated abundance of 36 roe deer with a sex ratio of 1.5 : 1 in favor of males. In most characteristics it differs from the remaining areas, i. e, around 500 male red deer typically reside and graze in this area, which was the main reason for distinguishing this locality as a separate sample.

The "Zrenjanin" area is a composite sample (25 individuals) obtained from 6 game districts lying within 40 km from "Zrenjanin" (45°20′ N, 20°50′ E) between the Tisa and Tamiš Rivers. The roe deer is dominant on an area of approximately 175,000 ha, with an estimated density of 3 ind. per 100 ha. Around 70% of the area is comprised of arable land under various cultures on chernozem soils, with mixed broad-leaved forests (variously degraded) comprising a minority of 10% within the alluvial plains of rivers.

Both the "Bački Monoštor" and "Zrenjanin" areas are under 90 m altitude. Both areas are under the influence of the pannonian semicontinental climate.

The "Severni Kučaj" area (44°30′ N, 21°50′ E) is a hunting ground of 21,507 ha, completely forested (>95%), its altitude ranging from 200–600 m, and under the influence of a continental climate – a hilly landscape with well-developed soils (brown forest soils and podzols) and a dominance of submontane beech forests (ass. *Fagetum submontanum*). Roe deer are present with an estimated density of 0.3 ind. per 100 ha with a sex ratio of 1 : 2 in favour of females. The estimated capacity of 300–500 heads is never reached due to over-exploitation by poaching. Red deer are also present at a comparable density, and are, in contrast to the roe deer, close to the projected capacity as a result of more effective management. 21 individuals were obtained from this area.

The "Negotin" hunting area (44°15′ N, 22°20′ E) is a hilly mountainous area of 96,423 ha on an altitude range under 1,100 m and under the influence of a continental climate. Soil types vary from brown acid soils on silicates to rendzinas on limestone. About 50% of the area is arable land, with pastures and meadows (25%) and forests (25%) covering the rest. Forests are mostly oak and hornbeam-ash forests (ass. *Quercetum frainettocerris, Carpinetum orientalis serbicum*) in lower, and montane oak and beech forests in higher elevations (ass. *Quercetum montanum, Fagetum montanum serbicum*). Roe deer are present at an estimated density of 4 ind. per 100 ha and are well managed. Red deer are present at low densities in adjacent regions. A total of 18 individuals was taken from this area.

In sum, a total of 94 specimens (188 genomes) has been analysed. The samples were taken during the regular hunting season in 1993 and 1994. Small samples of liver, kidney and muscle were removed immediately during field dressing, or very shortly after the animal was shot, and stored adequately labelled on ice. The samples were frozen prior to the analyses and kept at –25 °C to –30 °C. Techniques of horizontal starch gel electrophoresis and protein staining techniques were performed according to the procedures of Selander et al. (1971) and Ayala et al. (1972), with minor modifications. The 33 protein loci examined and buffer conditions used are listed in table 1. The most common allele was designated

Table 1. Survey of protein loci and electrophoretic conditions analysed in the roe deer.

No.	Protein*	Loci;	Enzyme commission number*	Electroforetic conditions**
1.	Alcohol dehydrogenase	Adh^+	1.1.1.1.	6
2.	α-Glycerophosphate dehydrogenase	α-Gpd, α-Gpd2	1.1.1.8	6
3.	Sorbitol dehydrogenase	Sdh^+, Sdh^-	1.1.1.14	6
4.	L-Lactate dehydrogenase	Ldh-1, Ldh-2	1.1.1.27	5
5.	Malate dehydrogenase	Mdh-1, Mdh-2	1.1.1.37	4
6.	Malic enzyme	Me-1, Me-2	1.1.1.40	2
7.	Isocitrate dehydrogenase	Idh-2	1.1.1.42	2
8.	6-Phosphogluconate dehydrogenase	6-Pgd	1.1.1.44	4
9.	Octanol dehydrogenase	Odh^-	1.1.1.73	5
10.	Xanthine dehydrogenase	Xdh	1.2.2.37	3
11.	NADH-diaphorase	Dia	1.6.2.2	5
12.	Superoxide dismutase	Sod-1, Sod-2	1.15.1.1	2
13.	Creatine kinase	Ck	2.7.3.2	2
14.	Adenylate kinase	Ak	2.7.4.3	2
15.	Phosphoglucomutase	Pgm-1, Pgm-2	2.7.5.1	5
16.	Esterase	Est-1, Est-2, Est-3	3.1.1.1	1
17.	Peptidase	Pep-1, Pep-2, Pep-3, Pep-4	3.4.1.1	4
18.	Carbonic anhydrase	Ca	4.2.1.1	3
19.	Mannosephosphate isomerase	Mpi	5.3.1.8	3
20.	Glucophosphate isomerase	Gpi	5.3.1.9	4
21.	Protein	Pt	–	1

* Nomenclature Commitee of the International Union of Biochemistry (1984).
** (1) Lithium hydroxide; (2) Tris-citrate pH 8; (3) Tris-versene-borate; (4) Phosphate-citrate; (5) Tris-maleate pH 7.4; (6) Tris-boric acid for dehydrogenase pH 9.

as 100 and other alleles were assigned numbers corresponding to the relative mobility of their respective allozymes. All variants having mobilities similar enough to preclude consistent separation were conservatively scored as the same allele. No electrophoretic differences between males and females have been found and hence no record on the sex ratio in the samples has been kept.

Allozyme data were analysed with the statistical package BIOSYS-1 (SWOFFORD and SELANDER 1981), using single-locus genotypes as input data for estimating parameters of genetic structure and the extent of genetic differentiation between populations. NEI's (1978) distance coefficient was clustered by the unweighted pair-group method (UPGMA: SNEATH and SOKAL 1973) to provide an overview of the genetic relationships among the samples.

In addition to WRIGHT's (1965, 1978) standard F-statistics, used to describe genetic structure of the analysed populations, indirect estimates of gene flow among populations were obtained using the procedures described in GONZÁLES-CANDELAS et al. (1992): WEIR and COCKERHAM's (1984) modification of F-statistics estimates; WRIGHT's (1943) method for estimate the gene flow level based on F_{ST} coefficient values and the "private alleles" method (SLATKIN 1985).

Results

Screening of 21 enzyme systems (a total of 33 presumptive structural loci) revealed polymorphism at the following 12 loci: Sdh+, Mdh-1, Me-1, Idh-2, 6-Pgd, Gpd-1, Ak, Pgm-1,

Table 2. Allele frequencies for five populations at 12 polymorphic loci in the roe deer. 1 = Bački Monoštor; 2 = Kozara; 3 = Zrenjanin; 4 = Severni Kučaj; 5 = Negotin.

	Population				
Locus (N)	1 (15)	2 (15)	3 (25)	4 (21)	5 (18)
Sdh 100	1.000	0.800	1.000	1.000	0.861
110	0.000	0.200	0.000	0.000	0.139
Mdh-1 90	0.000	0.000	0.080	0.000	0.000
100	1.000	0.733	0.920	1.000	1.000
110	0.000	0.267	0.000	0.000	0.000
Me-1 100	1.000	1.000	0.980	1.000	0.972
102	0.000	0.000	0.020	0.000	0.028
Idh-2 90	0.000	0.267	0.000	0.000	0.028
100	1.000	0.733	1.000	1.000	0.972
6-Pgd 95	0.033	0.000	0.000	0.000	0.000
100	0.933	1.000	0.920	1.000	1.000
110	0.033	0.000	0.080	0.000	0.000
α-Gpd 90	0.000	0.000	0.042	0.071	0.056
95	1.000	1.000	0.958	0.857	0.889
100	0.000	0.000	0.000	0.000	0.000
105	0.000	0.000	0.000	0.071	0.056
Ak 100	1.000	0.733	0.980	1.000	1.000
105	0.000	0.267	0.020	0.000	0.000
Pgm-1 94	0.033	0.000	0.060	0.000	0.000
100	0.967	1.000	0.940	1.000	1.000
Pgm-2 92	0.067	0.000	0.020	0.000	0.000
100	0.933	1.000	0.980	1.000	1.000
Ca 95	0.100	0.033	0.040	0.000	0.000
100	0.900	0.967	0.960	1.000	1.000
Mpi 100	0.933	1.000	0.960	1.000	1.000
106	0.067	0.000	0.040	0.000	0.000
Gpi 95	0.000	0.000	0.000	0.048	0.000
100	1.000	1.000	0.860	0.952	0.833
108	0.000	0.000	0.140	0.000	0.167

Pgm-2, Ca, Mpi and Gpi (Tab. 2). In all cases heterozygote band patterns were consistent with the known quaternary structure of the enzyme concerned (HARRIS and HOPKINSON 1976; HARRIS 1980). The following 21 loci were monomorphic: Adh, Sdh$^-$, Ldh-1, Ldh-2, Mdh-2, Me-2, Odh$^-$, Gpd-2, Xdh, Dia, Sod-1, Sod-2, Est-1, Est-2, Est-3, Pep-1, Pep-2, Pep-3, Pep-4 and Pt.

The deviation of genotype frequencies from Hardy-Weinberg equilibrium was estimated by the Chi-square test, modified by LEVENE's (1949) correction for small samples. Statistically significant deviations from equilibrium were obtained for the "Kozara" and "Severni Kučaj" populations. Eight loci showed statistically significant deviations from the Hardy-Weinberg distribution in at least one sample (Gpd-1 – in all samples except "Bački Monoštor"; Gpi – "Severni Kučaj", "Zrenjanin"; Pgm-1 – "Zrenjanin"; Sdh, Mdh-1, Idh-2, Ak, 6-Pgd – "Kozara").

Parameters of genetic variation are given in table 3. The proportion of polymorphic loci varied between 3.0 per cent and 12.1 per cent. The populations south of the Danube seem to be less polymorphic (3.0 per cent and 9.1 per cent) than the populations north of the Danube (all populations have 12.1 per cent polymorphic loci). Average heterozygosity per locus varied between 0.2 per cent and 2.0 per cent. The lowest genetic variability level characterized the sample from "Kozara", a subarea of "Bački Monoštor".

Table 3. Genetic variability at 33 loci in five populations of roe deer. (standard errors in parentheses)

Population	Mean sample size per locus	Mean no. of alleles per locus	Percentage of loci polymorphic*	Mean heterozygosity	
				Directcount	HdyWbg expected**
1. BAČKI MONOŠTOR	15.0 (.0)	1.2 (.1)	12.1	0.020 (.009)	0.019 (.009)
2. KOZARA	15.0 (.0)	1.2 (.1)	12.1	0.002 (.002)	0.049 (.022)
3. ZRENJANIN	25.0 (.0)	1.3 (.1)	12.1	0.016 (.005)	0.031 (.010)
4. SEVERNI KUČAJ	21.0 (.0)	1.1 (.1)	3.0	0.004 (.004)	0.011 (.008)
5. NEGOTIN	18.0 (.0)	1.2 (.1)	9.1	0.015 (.008)	0.026 (.013)

*A locus is considered polymorphic if the frequency of the most common allele does not exceed 0.95
** Unbiased estimate (see NEI 1978)

NEI's (1978) unbiased genetic distance coefficients varied between 0.000 and 0.007 (Tab. 4). The largest genetic distance was obtained between population "Kozara" and all the others and the least was noted between the two rather distant populations from Vojvodina (Pannonian plain). The genetic distances between our four populations (except "Kozara") correspond to their geographical distribution.

Table 4. Nei's unbiased genetic similary (above diagonal) and distance (below diagonal) for five roe deer populations.

Population	1	2	3	4	5
1. BAČKI MONOŠTOR	*****	0.993	0.999	0.999	0.998
2. KOZARA	0.007	*****	0.993	0.993	0.994
3. ZRENJANIN	0.001	0.007	*****	0.999	0.999
4. SEVERNI KUČAJ	0.001	0.007	0.001	*****	0.999
5. NEGOTIN	0.002	0.006	0.001	0.001	*****

Table 5. Contigency chi-square analysis among all analysed roe deer populations from north-eastern Yugoslavia. n. s = non-significant, *P < 0.05, **P < 0.01, ***P < 0.001.

Locus	allele	All five populations		
		χ^2	df	P
Sdh	2	22.359	4	***
Mdh-1	3	54.976	8	***
Me-1	2	2.518	4	n. s.
Idh-2	2	37.960	4	***
6-Pgd	3	13.822	8	n. s.
α-Gpd	3	11.628	8	n. s.
Ak	2	37.790	4	***
Pgm-1	2	6.158	4	n. s.
Pgm-2	2	6.716	4	n. s.
Ca	2	7.180	4	n. s.
Mpi	2	6.158	4	n. s.
Gpi	3	23.541	8	**
Total		230.796	64	***

The results of UPGMA clustering showed that the populations north of the Danube River cluster together with respect to the populations south of the Danube and that is in accordance with the existence of a geographical barrier represented by the Danube River (Fig. 2). The distribution of allele frequencies differed significantly among populations for 45% of analysed polymorphic loci (Tab. 5) indicating significant overall genetic heterogeneity.

When the "Kozara" sample was excluded from the analysis due to its specific position in the dendrogram, the distribution of allele frequencies among the remaining four populations did not differ significantly among samples for 75% of the polymorphic loci, but showed a total significant departure from randomness (Tab. 6). When only samples from area north of the Danube River ("lowland" populations) were subjected to analysis, the overall distribution of allele frequencies suggested absence of spatial heterogeneity. For the subset of samples south of the Danube River ("highland" populations), an overall significant genetic heterogeneity was again noted (Tab. 6).

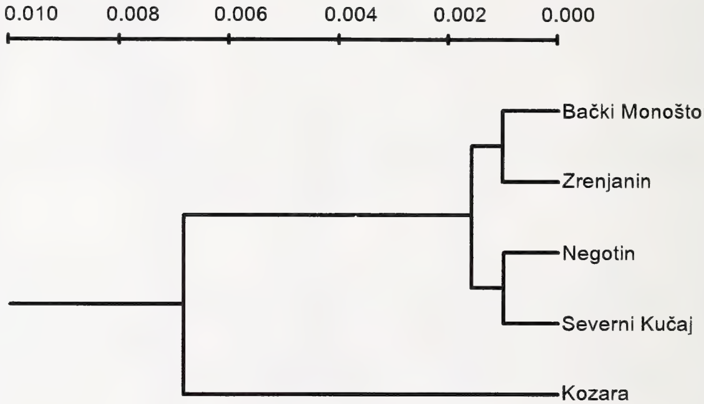


Fig. 2. UPGMA dendrogram of Nei's genetic distance for five roe deer populations.

The measure of the amount of genetic heterogeneity at all loci among the five sampling localities was calculated using WRIGHT's (1965, 1978) F-statistics (F_{ST}, F_{IS} and F_{IT}), quantifying the amount of inbreeding at different levels of nesting (Tab. 7). F_{IS} indicated statistically significant heterozygote deficiency (positive F_{IS} values) for most loci. For four loci (Me-1, Pgm-2, Ca and Mpi) there were negative F_{IS} values (excess heterozygosity) but without statistical significance. The highest positive value of F_{IS} was obtained for the Ak locus (0.907) and the highest negative value was for the Me-1 locus (–0.025). The mean value of F_{IS} for all loci was 0.564. The high positive value of F_{IS} for all loci suggests

Table 6. Contigency chi-square analysis among four roe deer populations from north-eastern Yugoslavia. ("Kozara" sample excluded).
n. s = non-significant, *P < 0.05, **P < 0.01, ***P < 0.001.

Locus	allele	Four populations			Lowland populations			Highland populations		
		χ^2	df	P	χ	df	P	χ^2	df	P
Sdh	2	10.363	3	*	/	/	/	3.640	1	n. s.
Mdh-1	2	8.864	3	*	2.526	1	n. s.	/	/	/
Me-1	2	1.797	3	n. s.	0.608	1	n. s.	1.182	1	n. s.
Idh-2	2	3.410	3	n. s.	/	/	/	1.182	1	n. s.
6-Pgd	3	10.666	6	n. s.	2.324	2	n. s.	/	/	/
α-Gpd	3	7.762	6	n. s.	1.283	1	n. s.	0.175	2	n. s.
Ak	2	2.174	3	n. s.	0.608	1	n. s.	/	/	/
Pgm-1	2	4.542	3	n. s.	0.281	1	n. s.	/	/	/
Pgm-2	2	5.174	3	n. s.	1.131	1	n. s.	/	/	/
Ca	2	7.237	3	n. s.	1.152	1	n. s.	/	/	/
Mpi	2	4.542	3	n. s.	0.281	1	n. s.	/	/	/
Gpi	3	17.308	6	**	4.608	1	*	9.020	2	*
Total		83.839	45	***	14.795	11	n. s.	15.199	7	*

the possibility that either selection or non-random mating or both caused an excess of homozygosity. Estimates of standardized variance of gene frequencies (F_{ST}) varied between 0.015 and 0.204 with a mean of 0.110. This value was also obtained by Hartl et al. (1991) for all populations from Hungary, Austria and Switzerland.

Indirect estimates of gene flow among populations obtained according to Weir and Cockerham's (1984) procedure (based on the degree of subdivision between populations, F_{ST}) was 2.70 migrants per generation (Tab. 8). By using their modification for loci, its value varied between 2.38 and 2.73, while using the modification for populations, the average number of migrants per generations varied between 3.06 and 4.14. The "private alleles" method (Slatkin 1985) showed a gene flow level of 12.26 migrants per generation. Using various modifications for loci its value varied between 17.62 and 46.78, while using modifications for populations the average number of migrants per generations varied between 22.31 and 27.95 (for commentary about modifications see Gonzáles-Candelas et al. 1992). All estimates of Nm were larger than 1, indicating that gene flow keeps populations from drifting to fixation.

Table 7. Summary of F-statistics at all loci for five roe deer populations.

Locus	F_{IS}	F_{IT}	F_{ST}
SDH	0.702	0.736	0.115
MDH-1	0.851	0.878	0.177
ME-1	–0.025*	–0.010*	0.015*
IDH-2	0.875	0.900	0.197
6-PGD	0.221	0.255	0.043*
α-GPD	0.735	0.747	0.046*
AK	0.907	0.926	0.204
PGM-1	0.398	0.418	0.032*
PGM-2	–0.059	–0.018*	0.039*
CA	–0.079	–0.036*	0.040*
MPI	–0.060	–0.022*	0.036*
GPI	0.570	0.605	0.083
Mean	0.564	0.612	0.110

*-coefficient is significant at P < 0.05

Discussion

Genetic variability in the roe deer from northeast Yugoslavia is lower than in populations from central Europe (Switzerland, Austria, Hungary), reported by Hartl et al. (1991). Also, genetic variability in Bulgarian, Slovenian and Slovakian roe deer is high when compared to the populations from Austria, Switzer-

Table 8. Estimates of Nm and their variances using two different methods for roe deer for 12 loci and 5 populations.

Estimate	loci/populations	p(1)	F_{ST}
Direct		12.26	2.70
Jackknife	loci	17.62	2.73
	populations	22.31	4.14
Variance	loci	442.81	0.10
	populations	401.77	16.10
Less biased	loci	46.78	2.38
	populations	27.95	3.06

land, France, and Hungary (Hartl et al. 1993). J. Ernhaft (pers. comm.) reported for the Hungarian roe deer populations a proportion of polymorphic loci of 11.27 per cent and expected average heterozygosity of 3.84 percent. Milošević (1986) obtained a value of mean heterozygosity of 10.0 per cent and polymophism level of 31.0 percent for the populations of roe deer from central Yugoslavia. Those values are higher than in the present study. Apart from computational differences, different loci were sampled which contributed to this difference.

Our values of the proportion of polymorphic loci and expected average heterozygosity for the populations from Vojvodina, the southern part of the Pannonian plain, are of the order presented for the populations from Hungary which is the closest neighboring area (P = 12.1 per cent v. s. 13.0 percent; Hmean = 3.3 per cent v. s. 3.7 per cent; reported by Hartl et al. 1991, 1993; and P = 12.1 per cent v. s. 11.3 per cent; Hmean = 3.3 per cent v. s. 3.8 percent; reported by J. Ernhaft, pers. comm.). Compared with Bulgarian populations, the values for the populations from the eastern part of Serbia are lower (P = 6.1 percent v. s. 17.5 percent; Hmean = 1.9 per cent v. s. 6.5 per cent; Hartl et al. 1993).

For the samples from "Kozara" and "Severni Kučaj" we obtained low genetic variability compared to the other analysed populations. Our explanation could support the hypothesis that genetic variability level is mostly dependent on parameters of the population structure such as population density and effective population size. According to Soulé (1976), heterozygosity is largely determined by population size; more precisely, Simanek (1978) argued that effective population size determines the level of heterozygosity. Those arguments are well reflected in our data, i. e., the populations from "Kozara" and "Severni Kučaj". In these two populations we believe that game management techniques (enclosure, competition, overexploitation) directly influence effective population size and lead to observed loss of genetic variability. These factors do not operate in the other populations of this study which are more effectively managed. Similar to the study by Hartl et al. (1993), sample groups belonging to different ecotypes ("field" vs. "forest") did not show genetic distance higher than those typical for local populations.

Our results on the level of gene flow, based on both F_{ST} and "private" alleles estimates, are of the same order, especially when compared to values reported for subdivision of population groups of the same species (2.66, 3.92, 1.67; Hartl et al. 1991). They are, however, higher than the values for the Hungarian populations ("Eastern group"), 2.70 : 1.67, but lower than those reported for four Bulgarian populations (5.43, Hartl et al. 1993). Our examined populations lie geographically in the transect Hungary-Bulgaria and are pannonian ("Bački Monoštor" and "Zrenjanin") and perirhodopic ("Severni Kučaj" and "Negotin"). We note that the transect Hungary, Yugoslavia, Bulgaria has growing rates of gene flow (1.67, 2.70, 5.43).

This could be relevant to HARTL's et al. (1991) discussion on the existence of, broadly speaking, a north-south gradient in roe-deer population differentiation (Hungary, Yugoslavia, Bulgaria). We would argue that this gradient is not only geographical (longitudinal) but also reflects the transition between lowland (predominantly agricultural) to highland landscapes with, we believe, an adequate shift in game management activities. On the local level, the Danube River does not represent a strong migration barrier, although we observed a difference in the average number of migrants per generation between lowland "Bački Monoštor" – "Zrenjanin"and highland "Severni Kučaj" – "Negotin" subgroups. The spatial distribution of allele frequencies also has a different pattern among lowland (sample from "Kozara" excluded) compared to highland samples. Allele frequencies for most polymorphic loci are randomly distributed among localities north of the Danube River, while in the highland area (south of the Danube River) less loci are in polymorphic condition and the overall spatial distribution of their allele frequencies is significantly non-random. Nevertheless, with genetic distance values of up to 0.007 and the lack of clear differences in allele types on homologous loci, there is no evidence of subspecific differentiation on the level of genic-enzymatic systems (see: HARTL et al. 1991).

An overall assessment of the factors determining the genetic structure of roe deer populations in this part of the range is that there is no evidence of genetic drift, implying selection or non-random mating as important factors. Our data provide some evidence for the existence of a north-south selection gradient, clinal in nature. Spatial heterogeneity exists south of the Danube River barrier and is located within the highland areas. Inadequate game management significantly alters population structure in two populations ("Kozara", "Severni Kučaj"). Our data suggest that non-random mating (strengthened by game management-exploitation, reproductive behavior and territoriality, adaptation to semiurban habitat complexes) is probably more important than selection in influencing population genetic structure.

The small number of populations analysed in this study and their heterogeneity in regard to effective population size, game management, and habitat type do not give us adequate opportunity to analyse in greater detail the genetic structuring of populations in this part of species range and the influence of various factors on possible differentiation within species. However, additional samples from both lowland and highland regions of Yugoslavia will make possible the testing of various hypotheses about roe deer population structure. As THORPE (1980) suggested, for recognizing the possible subtle racial differences within species one should investigate also the variation of external morphology. We suppose that a combination of biochemical, craniometric and morphometric analyses, will give a clearer impression of the status of Yugoslavian roe deer populations.

Acknowledgements

We are grateful to Prof. Dr. LUCIANO BULLINI and Dr. GIUSEPPE NASCETTI from the Dipartimento di Genetica e Biologia Molecolare dell Universita di Roma "La Sapienza" in whose laboratories we performed a portion of our analyses. We acknowledge the help of Ing. MIHAJLO HADŽI-PAVLOVIĆ, M. Sc. (National Park "Đerdap", Yugoslavia), Ing. MIHALJ KALINKA, M. Sc. (JP "Srbijašume-Kozara", Bački Monoštor, Yugoslavia), Ing. SLOBODAN KASTRATOVIĆ (hunters association "Hajduk Veljko", Negotin, Yugoslavia), and IVAN TADEIN (Zrenjanin, Yugoslavia) for collecting samples over the last few years. This work was financed by Grant No. 0321 of the Ministry of Science and Technology of Serbia, Yugoslavia.

Zusammenfassung

Genetische Variabilität von Rehpopulationen (Capreolus capreolus L.) aus dem nordöstlichen Jugoslawien

Gewebeproben von 94 Rehen (*Capreolus capreolus* L.) aus fünf Populationen in Jugoslawien wurden mittels horizontaler Stärkegelelektrophorese auf genetische Variabilität und Differenzierung an 33 hypothetischen Strukturgenloci untersucht. Die Polymorphierate schwankte zwischen 3,3% und 12,1%, der durchschnittliche Heterozygotiegrad zwischen 0,2% und 2%. Die Schätzwerte für die standardisierte Varianz der Genfrequenzen (F_{ST}) reichten von 0,015 bis 0,204, mit einem Mittelwert von 0,110. Indirekte Schätzungen des Genflusses zwischen Subpopulationen bewegten sich zwischen 2,7 (nach der F_{ST}-Methode) und 12,26 (nach der „Private-Allele-Methode") Migranten pro Generation. Die Populationen im Hochland südlich der Donau zeigten signifikante Unterschiede in den Allelfrequenzen. Die Angaben über Polymorphieraten, Heterozygotiergrade und Genflußraten liegen innerhalb des von anderen Autoren bei ungarischen und bulgarischen Populationen gefundenen Bereichs. Nach unseren Daten wird die genetische Struktur der Populationen im Untersuchungsgebiet weniger durch genetische Drift als durch Selektion oder Abweichungen von der Zufallspaarung bestimmt. Unter Berücksichtigung publizierter Daten läßt sich beim Reh eine Nord-Süd-Kline in den populationsgenetischen Grundparametern erkennen.

References

Ayala, F.; Powell, J. R.; Tracey, M. L.; Mourao, C. A.; Parez-Salas, S. (1972): Enzyme variability in the *Drosophila willistoni* group. IV. Genetic variation in natural populations of *Drosophila willistoni.* Genetics **70**, 113–139.

Gonzáles-Candelas, F.; Crnobrnja J.; Kalezić, L. M.; Moya, A. (1992): Gene flow rates in Yugoslavian populations of the smooth newt *Triturus vulgaris.* J. Evol. Biol. **5**, 481–490.

Harris, H. (1980): The Principles of Human Biochemical Genetics. Amsterdam: Elsevier/North Holland.

Harris, H.; Hopkinson, D. A. (1976): Handbook of Enzyme Electrophoresis in Human Genetics. Amsterdam: Elsevier/North Holland.

Hartl, G. B.; Reimoser, F. (1988): Biochemical variation in roe deer (*Capreolus capreolus* L.): are r-strategists among deer genetically less variable than K-strategists? Heredity **60**, 221–227.

Hartl, G. B.; Reimoser, F.; Willing, R.; Köller, J. (1991): Genetic variability and differentiation in roe deer (*Capreolus capreolus* L.) of Central Europe. Gen. Sel. Evol. **23**, 281–299.

Hartl, G. B.; Markov, G.; Rubin A.; Findo, S.; Lang, G.; Willing, R. (1993): Allozyme diversity within and among populations of three ungulate species (*Cervus elaphus, Capreolus capreolus, Sus scrofa*) of Southeastern and Central Europe. Z. Säugtierkunde **58**, 352–361.

Levene, H. (1949): On a matching problem arising in genetics. Ann. Math. Stat. **20**, 91–94.

Milošević, S. (1986): Intraspecijska diferencijacija srne (*Capreolus capreolus* L.), M. Sc. thesis, PMF, Beograd.

Milošević-Zlatanović, S.; Savić, R., I.; Stamenković, S. (1994): Genetic divergence in the roe deer (*Capreolus capreolus* L.) in Yugoslavia. Bios **2**, 307–314.

Nei, M. (1978): Estimation of average heterozigosity and genetic distance from a small number of individuals. Genetics **89**, 583–590.

Nomenclature Commitee of the International Union of Biochemistry (1984): Enzyme nomenclature. New York: Academic press.

Ryman, N.; Baccus, R.; Reuterwall, C.; Smith, H. M. (1980): Effective population size, generation interval, and potential loss of genetic variability in game species. Oikos **36**, 257–266.

Selander, R. K.; Smith, H. M.; Yang S. Y.; Yohnson, W. E.; Gentry, J. B. (1971): Biochemical polymorphism and systematics in the genus *Peromyscus.* I. Variation in the old-field mouse (*Peromyscus polionatus*), Studies in Genetics VI, Univ. of Texas Publ. **7103**, 49–90.

Simanek, D. E. (1978): Genetic variability and population strucure of *Poecilia latapinna.* Nature **276**, 612–614.

Slatkin, M. (1985): Rare alleles as indicators of gene flow. Evolution **39**, 53–65.

Sneath, P. H.; Sokal, R. R. (1973): Numerical Taxonomy: the principles and practice of numerical classification. San Francisco: Freeman and Co.

SOULÉ, M. (1976): Allozyme variation: its determinants in space and time. In: Molecular Evolution. Ed. by F. J. AYALA, Sunderland, Mass.: Sinauer Ass. P p. 60–77.

SWOFFORD, D. L.; SELANDER, R. B. (1981): Biosys 1. A Fortran program for the comprehensive analysis of electrophoretic data in population genetics and systematics J. Hered. **72**, 281–283.

THORPE, R. S. (1980): Microevolution and taxonomy of European reptiles with particular reference to the grass snake *Natrix natrix* and the wall lizards *Podarcis sicula* and *P. melisellensis.* Biol. J. Linn. Soc. **14**, 215–233.

WEIR, B. S.; COCKERHAM, C. C. (1984): Estimating F-statistics for the analysis of population structure. Evolution **38**, 1358–1370.

WRIGHT, S. (1943): Isolation by distance. Genetics **28**, 114–138.

WRIGHT, S. (1965): The interpretation of population structure by F-statistics with special regard to systems of mating. Evolution **9**, 395–420.

WRIGHT, S. (1978): Evolution and Genetics of Populations. Vol. 4. Variability within and among natural populations. Chicago: Univ. Chicago Press.

Authors' addresses: SVETLANA MILOŠEVIĆ-ZLATANOVIĆ, M. Sc., Institute of Biology, Faculty of Science, University of Kragujevac, Radoje Domanovića 12, Yu-34000 Kragujevac, FR Yugoslavia, JELKA CRNOBRNJA-ISAILOVIĆ, M. Sc., Institute for Biological research "Siniša Stankovič", 29. novembra 143, Yu-11000 Beograd, FR Yugoslavia, Prof. Dr. Ivo R. SAVIĆ, and SRDJAN STAMENKOVIĆ, M. Sc., Institute of Zoology, Faculty of Biology, University of Belgrade, Studentski trg 16, Yu-11000 Beograd, FR Yugoslavia.

Z. Säugetierkunde **62** (1997) 350–358

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Experimental colonisation of contrasting habitats by house mice

By Françoise H. Tattersall, R. H. Smith, and F. Nowell

Department of Pure and Applied Zoology, University of Reading, Reading, United Kingdom

Receipt of Ms. 29. 10. 1996
Acceptance of Ms. 12. 03. 1997

Abstract

House mice (*Mus domesticus*) are successful colonists, thriving both indoors and outdoors in a wide range of habitats, with the general exception of woodland. We investigated some of the processes affecting house mouse colonisation success by comparing the fates of mice experimentally introduced into woodland or buildings and provided with food and shelter (straw stacks) at a focal point. House mice introduced into buildings generally became established and bred, while house mice introduced into woodland declined to extinction within three months. House mice in buildings radiated away from the stacks and some established in the surrounding grassland, while house mice in woodland rarely left the stacks. At buildings captures of house mice outdoors correlated negatively with captures of wood mice (*Apodemus sylvaticus*). There was evidence of heavy predation by weasels (*Mustela nivalis*) on house mice in woodland, but not in buildings. We suggest that woodland was unsuitable for house mice due to a combination of competition and predation: competition with wood mice restricted house mice to their focal introduction point making them vulnerable to extinction through predation by weasels.

Introduction

Colonisation can be defined as a process which starts with the arrival of a propagule in a new habitat patch, and ends when the probability of extinction is no longer dependant on propagule properties (Ebenhard 1991). The house mouse (*Mus domesticus*) is a highly successful colonist, being one of the most widespread of all mammals (Meehan 1984). There are few studies relating specifically to colonisation of house mice, but the unsuccessful attempts of Berry et al. (1982) to introduce them to the Shetland Isles suggest that even for this species, colonisation is not always a simple process.

House mice have become established in an enormous range of environmental conditions, living both ferally and commensally (Berry 1981). Woodland, however, is one habitat in which records of house mice living independently from man are scarce throughout the world. An exception is woodland in New Zealand, where no other small rodents are present (Fitzgerald et al. 1981; King 1982), but even these house mouse populations live at very low densities (0.6–3.3 per hectare). House mice have adapted to almost every conceivable climate (Berry 1981) and so it is unlikely that they are prevented from colonising woodlands by an abiotic variable.

In southern England several factors could prevent house mice from colonising woodland. For example, they might not range widely enough to encounter woodland sufficiently regularly, and are unlikely to be translocated there by man. We investigated some of the processes affecting colonisation success of house mice introduced into favoured habitat (buildings) and into apparently sub-optimal habitat (woodland). Using live-trapping we aimed to discover whether there were habitat-related differences in survival, breeding, and expansion, and whether these were mediated by predation or competition.

Material and methods

Study sites

Building sites were situated at a semi-derelict farm and horticultural station near Shinfield, Berkshire, UK. Outdoor sites were in University of Reading woodland near Shinfield, Berkshire, UK. Sites in buildings ranged from a small tin-roofed building, to an old stable block, to old chicken houses. All buildings were surrounded by rough grassland, concrete, and other buildings. Woodland areas were predominantly mixed deciduous and coniferous, with some hazel (*Corylus avellana*) coppice. House mice were not present at any site prior to the experimental releases, but there was movement of small numbers of experimental animals between nearby building sites both within and between trials. Wood mice (*Apodemus sylvaticus*) were present at all sites, but not inside buildings.

Experimental releases

Eighteen groups of three male and nine female house mice bred from wild stock were individually marked by toe-clipping under Home Office licence, and one group was released into each of 18 straw stacks. Stacks were built with 12 bales of straw, and measured 1.5 m by 1 m around the base and 2 m high. Nine stacks were in derelict buildings and nine stacks were in woodland.

Releases of house mice took place in three trials (May 1991, November 1991, and March 1992), each using a different three building stacks and three woodland stacks. For each trial, the introduced animals were adults taken from the same stock and matched for sex and, so far as possible, for weight, in paired building and woodland stacks. However, the degree of relatedness, and the degree of social contact between animals introduced into a particular stack was not always known, and probably varied. Fighting among introduced males in particular would have been reduced if males had been housed together prior to release, or if they were siblings.

In all trials, pups up to two days old were introduced with their mothers because most of the other, non-suckling, females were heavily pregnant. Large numbers of pups were introduced in May (32 in buildings and 52 in woods); in November and March no more than 15 pups were introduced. Evidence considered later suggests that few of these extra individuals survived.

As well as an initial 1 kg of wheat scattered inside the stack, animals were provided with 1.75 kg wheat ad libitum from a covered food box placed next to the stack. This was renewed approximately every three weeks, and became depleted only in woodland stacks.

Monitoring

Changes in populations of house mice and naturally occurring wood mice were followed using Longworth live traps and capture-mark-release methods. The areas in and around the stacks were trapped both before and after introduction, at approximately three to four-week intervals until house mice were no longer being captured (9–23 weeks). Sixty traps were used: eight in and under the stack, four around the food box, a square of eight 1 m from the stack. The remainder were placed in three concentric squares consisting of eight, 16, and 16 traps, placed 5 m, 15 m and 20 m from the stack, with distances between traps of 5 m, 5 m, and 10 m respectively. This layout was adhered to as strictly as possible, but physical constraints imposed by walls meant that layout in buildings varied. Trapping sessions lasted for three nights. Within each trial, timing of introduction and trapping was exactly paired for building and woodland stacks.

Statistical tests

House mouse and wood mouse abundances were calculated as Minimum Number Alive (MNA). Newborn pups could not be included in these analyses until they became large enough to be captured and marked, at least three weeks after their introduction. In order to combine information from different trials data were tested for homogeneity using Chi-squared.

At each site we used regression analysis to calculate the slope of the change through time in numbers of all individuals and in numbers of original colonists. The total number of house mice at day 0 was the number introduced, that is, 12, and this number was excluded from the regression analysis for total

MNA, as a known number of mice was not comparable with an estimated number. The sudden drop in the number of house mice estimated one day after introduction in May supports this exclusion. The slopes of changes in numbers in buildings and woodland were compared by analysis of variance; sources of variation were habitat (building or wood) and month (May, November, and March).

We used body weight as a predictor of age, and divided all non-original individuals caught in a stack into three groups: (a) conceived in stack, (b) introduced into stack as a pup or as a foetus, and (c) migrant from an experimentally introduced population at a nearby stack. For example, 36 days after introduction, individuals conceived in the stack weighed less than 6 g, while those introduced into the stack as pups or foetuses weighed 7–10 g. Adults introduced into the stack weighed more than 15 g. Best estimates of numbers in each group took into account trap position (central or peripheral) and all weight recordings. Maximum and minimum estimates were produced by inclusion or exclusion of animals with first recorded weights on the borderline of one of the three groups. Data (in the form of counts) remained separate for each stack, and were transformed with a square root transformation prior to an ANOVA test. ANOVA was performed separately on best, maximum, and minimum estimates for individuals conceived, introduced, and total produced, with month (May, November, and March) and habitat (building or wood) as sources of variation.

At each site we calculated the proportion of all house mouse captures which occurred away from the stack, and the proportion of individuals which occurred away from the stack. We define 'away from the stack' as excluding traps in the area inside or under the stack, and the four traps around the food box. These proportions were then transformed using an angular transformation prior to ANOVA. Sources of variation were habitat (building or woodland) and month (May, November, and March). A similar analysis for wood mice used the presence or absence of house mice as a source of variation.

Results

Changes in numbers

The Minimum Number Alive (MNA) for house mice and wood mice was estimated at each site for each trapping session (Fig. 1). Using homogeneous data, after 10 days significantly more original colonists remained at woodland sites (83%) than building sites (39%; $X^2 = 30$, df = 1, $p < 0.001$). After 64 days, however, more original colonists remained in buildings (32%) than in woods (6%; $X^2 = 16$, df = 1, $p < 0.001$).

There was a significant difference in the slopes of change in total numbers of house mice in buildings and woods ($F_{(1,12)} = 22.7$, $p < 0.001$), with building slopes tending to be positive (mean slope = 0.01), and all woodland slopes being negative (mean slope = –0.11). Month of introduction had no effect on the slope, and there was no interaction between habitat and month.

Among original adult colonists only, ANOVA again showed that month had no effect, and there was no interaction between month and habitat. The effect of habitat, however, was again significant ($F_{(1,12)} = 11.44$, $p < 0.01$), with numbers in buildings declining less rapidly (mean slope = –0.06) than numbers in woodland (mean slope = –0.12).

Analysis using data only for original house mice was necessary because some captures on the building sites originated from previous introductions. It was also important to know whether differences in slopes of numbers of individuals arose from adult survival, from survival of pups introduced with their mothers, or from breeding success. The fact that both total numbers of individuals and numbers of original colonists declined faster in woodland than buildings suggests that adult survival was higher in buildings.

Production of young

There was no effect of habitat or month on the total number of individuals produced at each site, or on any estimate of numbers introduced as a pup or foetus. However, all estimates of numbers conceived in stacks showed an effect of habitat, with fewest individuals conceived in woods (for the best estimate $F_{(1,12)} = 8.35$, $p = 0.014$; for the maximum estimate $F_{(1,12)} = 8.69$, $p = 0.012$; for the minimum estimate $F_{(1,12)} = 5.11$, $p = 0.043$).

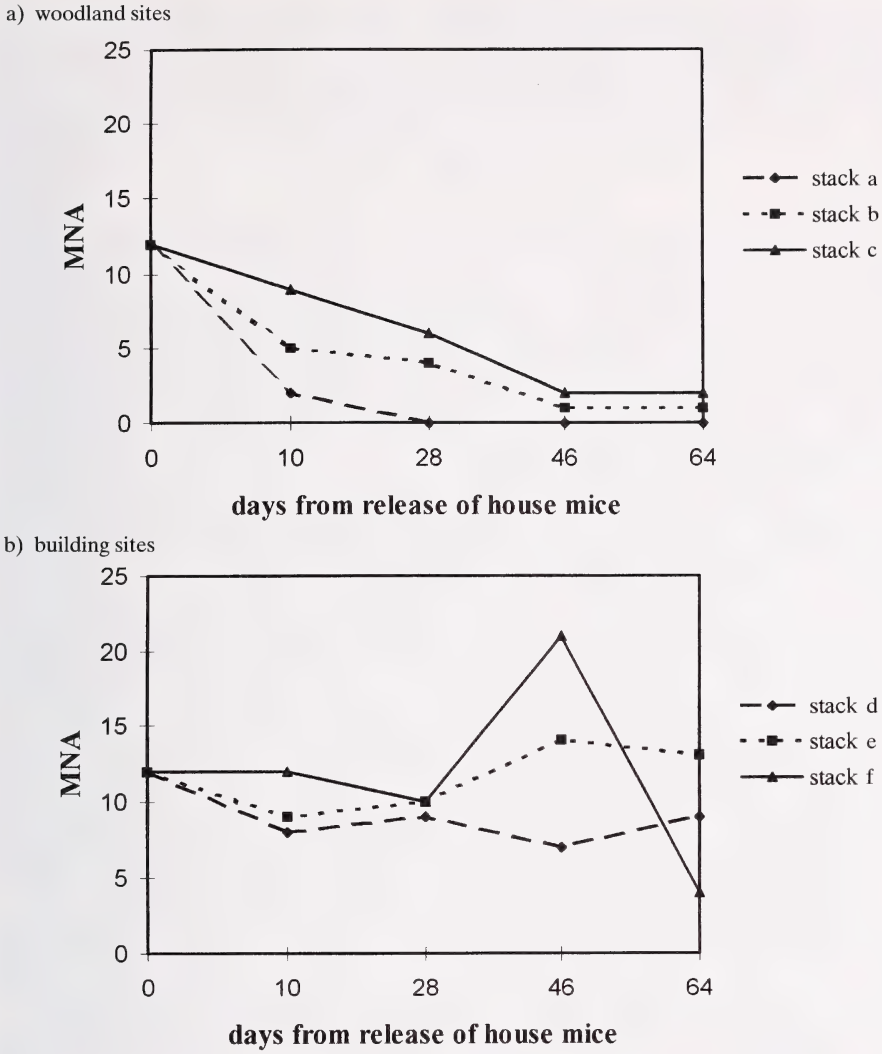


Fig. 1. Minimum Number Alive (MNA) estimates for house mice present at trapping sessions at a) woodland and b) building sites, using the November trial as an example. The number of house mice at day 0 was the number of adults introduced, that is, 12.

Equivalent numbers of young were, therefore, introduced as foetuses or pups to buildings and woodland and so growth of these extra individuals cannot account for differences in the rates of population change in the two habitats. The lack of differences between months, despite the fact that many more mice were introduced as pups or foetuses in May than in November or March, suggests that few of these extra individuals survived.

Range expansion

Habitat had a significant effect on proportions of both individuals and captures away from the stack ($F_{(1,12)} = 14.5$, $p = 0.003$ for individuals; $F_{(1,12)} = 15.8$, $p = 0.002$ for captures). There was a greater proportion of both captures and individual house mice caught

away from the stack at building sites (captures: 33.8%, n = 355; individuals: 54.4%, n = 136) than at woodland sites (captures: 7.1%, n = 411; individuals: 19.8%, n = 106) suggesting that expansion from the focal introduction point was greater in buildings than in woodland.

Wood mice

Wood mice were present at all sites, and were most abundant in November. No wood mice were caught inside the buildings, but they were caught around the outside edges of buildings. Overall, the average MNA at any one time at building sites (6.5) was slightly less than that in woods (9.2). However, wood mice on building grids had fewer traps available to them, because many traps were inside the buildings, and because the total building grid area was often less than total grid area in the woods as a result of constraints of trapping in and around buildings. Wood mouse populations outside buildings were, in fact, probably more dense than wood mouse populations in woodland: an average of 0.20 wood mice per trap-night (i. e. per trap outdoors per night) were caught at building sites, compared with an average of 0.15 in woodland.

At seven buildings surrounded by vegetation, there was a negative correlation between the number of captures of house mice and the number of captures of wood mice ($r = -0.945$, $df = 5$, $p < 0.01$) in traps placed outside the buildings (Fig. 2). At most sites there were more captures of wood mice than house mice.

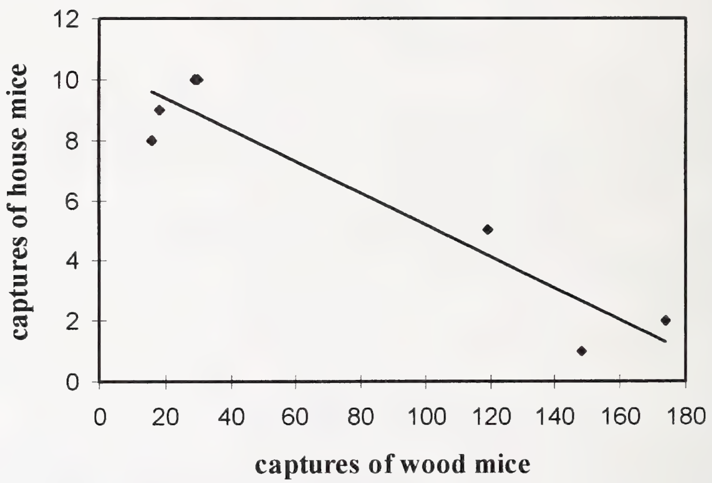


Fig. 2. The relationship between the number of captures of wood mice and house mice at trap points outside building sites surrounded by vegetation. There was a significant negative correlation between captures of house mice and captures of wood mice ($r = -0.945$, $df = 5$, $p < 0.01$).

No relationship between numbers of captures of wood mice and house mice was found at woodland sites. However, wood mice were more likely to use woodland stacks when house mice were absent than when they were present: a significantly greater proportion of wood mouse captures occurred in stacks when house mice were absent ($F_{(1,12)} = 12.99$, $p = 0.004$).

Predation

There was evidence of much higher predation levels at woodland sites than in buildings. Domestic cats were infrequently present at two building sites, and fox prints were occa-

sionally found inside a third. In contrast, both indirect signs (scats and paw prints) and direct sightings showed that weasels (*Mustela nivalis*), badgers (*Meles meles*), foxes (*Vulpes vulpes*), and tawny owls (*Strix aluco*) were present at all woodland sites. Eight stacks were dismantled in woodland and eight in buildings. While there were no signs of predation in building stacks, four (50%) of those dismantled in woodland contained weasel nests and scats. Weasels were twice accidentally captured in woodland stacks.

Discussion

Once an area has been reached, in our case by artificial translocation, successful establishment could be prevented by breeding failure or by short residency of immigrants. Residency could be reduced by emigration or death, for example in response to competition or predation. Doncastor (1992) has shown how predation influences where hedgehogs (*Erinaceus europaeus*) live. Hedgehogs transplanted into woodlands containing high densities of predators (badgers) suffered higher mortality and dispersed away from their release sites at greater rates than hedgehogs introduced into woodland without predators.

In apparently suitable habitats poor breeding success and/or short residency, could result from resource or interference competition (De Long 1966; Lidicker 1966). Resource competition with wood mice was implicated by Berry and Tricker (1969) as a reason for the extinction of the house mouse on the Scottish island of St. Kilda when the human population left. Bearing in mind that house mice are not indigenous over most of their geographic range, they are likely to be prone to competition from other small mammals, which may be more finely adapted to local conditions. Indeed, permanent populations of house mice are most common in areas where there are empty niches, such as species-impoverished islands (e. g. Berry 1964; Berry et al. 1979; Dueser and Porter 1986; Granjon and Cheylan 1988) or land disturbed by agriculture, mining or fire (e. g. Fox and Fox 1986; Breise and Smith 1973; Stickel 1979). In reciprocal removal experiments Fox and Pople (1984) and Fox and Gullick (1989) have shown that house mice are competitively inferior to the Australian *Pseudomys novaehollandiae*, except at very high densities.

Our experiments suggest that in the success or failure of establishment of house mouse populations in buildings and woodland depends, at least in part, on a subtle interaction between competitive exclusion by wood mice and predation, predominantly by weasels.

Adamkzyk and Ryskowski (1965), and Lidicker (1976), found that after introduction to an attic and enclosure respectively, house mice ranged widely initially, and then quickly showed strong site preferences. In our study, larger numbers of captures away from the stacks in buildings than in woods suggest that differences in losses of animals between the time of introduction and the first trapping session may be due to greater initial movement from buildings during the settling-in phase.

Subsequent establishment of some populations of introduced house mice in the vicinity of the buildings suggests that differences in capture rates away from stacks reflect a spreading out from the stack rather than dispersal away from the site. In the woods there was little evidence of emigration, with the majority of animals being caught in or around the stack. One exception was site 13, which had little canopy cover, but had particularly good ground cover, with a lattice-work of dead wood covered with cleavers (*Galium aparine*) surrounding the stack, which clearly aided movement of animals. However, seven of the eight individuals caught outside were subsequently recaptured in the stack. This provides further evidence that there truly was little emigration from woodland sites, rather than that emigrating animals dispersed away from an area very quickly and so were difficult to trap (Walkowa et al. 1989).

Differences in movement away from the stacks may have resulted in different spatial groupings, with house mice in woods living closer together, packed into the stack, and house mice in buildings being more scattered. Such spatial differences might affect aspects of social organisation, such as levels of aggression and reproduction (Pelikán 1981; Walkowa 1981), leading to the lower rates of recruitment observed in woodland. However, differences in the number of young conceived in buildings and woodland could also be an artefact of low adult survival in woodland.

Another, more severe, consequence of the spatial organisation of house mice in woods seems to have been increased vulnerability to extinction from predation. A small, sedentary group of house mice living at high density, as they were in woodland, would – once they had been found by a predator – be more susceptible to predation than scattered, mobile groups such as those in buildings. A small, nimble predator such as a weasel, which could enter the very heart of a stack, could easily and quickly kill the majority of the group. Our evidence shows that not only did weasels enter stacks, but they also made their nests in them.

Why did house mice in buildings move out of stacks, while house mice in woodland did not? One of the main differences between building and woodland sites was that there were far fewer predators present in the buildings. Lima and Dill (1990) argue that there is evidence that animals are able to asses their risk of predation, and make decisions about their feeding, social, or escape behavior accordingly. In woodland the presence of predators outside the stacks, and the lack of evidence for prior predator visits within the stacks, may have reduced the apparent risk of predation to mice which remained within the stacks. In buildings, where few or no predators were present, the risks from predation would have been similar in and out of the stacks.

A second difference was that there were no wood mice in the buildings, although they were present outside. Evidence from building sites indicates that movement of house mice was restricted by the presence of the abundant wood mice. At building sites house mice moved outside despite the presence of wood mice, but there was a negative correlation between captures of wood mice and house mice outside buildings. This correlation suggests either that house mice were not moving outdoors in areas where wood mouse numbers were high, or that there was competition for traps. However, the large number of wood mouse captures compared to house mouse captures, and the fact that at least 50% of traps remained unsprung each morning, support the idea that house mice actively avoided wood mice.

We have shown that even when provided with sufficient food and shelter, and artificially translocated in groups, house mice are unable to colonise English woodlands but colonise derelict buildings with ease. Large-scale ecological experiments in the field are extremely difficult, being costly, time-consuming, and hard to control. While our design allowed direct comparison of establishment success of house mice in buildings and woodland, it did not allow us to rigorously test for the effect of competition and predation. None the less, our data allow us to suggest that woodland was unsuitable for house mice due to an interplay between competition and predation: competition with wood mice restricted house mice to their focal introduction point making them vulnerable to extinction through predation by weasels. Experimental manipulations of house mice and their competitor and predator densities are required to fully test their effect on house mouse colonisation. However, our preliminary data point to some of the potential problems encountered by colonists and are relevant to wider question of how animals are distributed in space.

Acknowledgements

We would like to thank W. I. Montgomery for his comments on the manuscript, and Paul Beattie, Viv Lancaster and Javier Sanchez for their help in the field. The work was carried out while FHT was in receipt of a Science and Engineering Research Council grant.

Zusammenfassung

Experimentelle Kolonisation von gegensätzlichen Habitaten durch Hausmäuse

Hausmäuse (*Mus domesticus*) sind erfolgreiche Kolonisten. Sie besiedeln viele verschiedene Habitate und leben sowohl in Gebäuden als auch im Freien, generell jedoch nicht in Waldgebieten. Wir haben einige der Prozesse und Faktoren untersucht, die die erfolgreiche Besiedlung durch Hausmäuse beeinflussen, indem wir das Schicksal von Mäusen, die in Waldgebieten ausgesetzt wurden, mit dem von Mäusen verglichen haben, die in Gebäuden ausgesetzt wurden. Beiden Gruppen wurde jeweils an einem bestimmten Fokuspunkt Nahrung und Schutzmöglichkeit (Strohhaufen) angeboten. Während sich Hausmäuse in Gebäuden generell etablierten und fortpflanzten, starben die Hausmäuse im Wald innerhalb von drei Monaten wieder aus. Hausmäuse in Gebäuden verbreiteten sich ausgehend von den Strohhaufen und siedelten sich zum Teil im umliegenden Grasland an, während Hausmäuse in Waldgebieten die Strohhaufen nur selten verließen. In der Umgebung von Gebäuden korrelierte die Anzahl gefangener Hausmäuse negativ mit der Fangquote von Waldmäusen (*Apodemus sylvaticus*). In Waldgebieten, nicht jedoch in Gebäuden, wurde ein starker Beutedruck von Mauswieseln (*Mustela nivalis*) auf Hausmäuse beobachtet. Wir folgern, daß aufgrund einer Kombination von Konkurrenz- und Beutedruck Waldgebiete für Hausmäuse ungeeignet waren: Konkurrenz mit Waldmäusen beschränkte Hausmäuse auf das Gebiet, in dem sie ursprünglich freigelassen wurden und machte sie damit anfällig für Ausrottung durch Beutedruck von Mauswieseln.

References

Adamkzyk, K.; Ryskowski, L. (1965): Settling of mice (*Mus musculus* L.) released in an uninhabited and an inhabited place. Bulletin de l'Académie Polonaise des Sciences **13**, 631–637.

Berry, R. J. (1964): The evolution of an island population of the house mouse. J. Animal Ecol. **37**, 445–470.

Berry, R. J. (1981): Town mouse, country mouse: adaption and adaptability in *Mus domesticus* (*Mus musculus domesticus*). Mammal Review **11**, 91–136.

Berry, R. J.; Bonner, N. W.; Peters, J. (1979): Natural selection in house mice from South Georgia (South Atlantic Ocean). J. Zool. (London) **189**, 385–398.

Berry, R. J.; Cuthbert, A.; Peters, J. (1982): Colonisation by house mice: an experiment. J. Zool. (London) **198**, 329–336.

Berry, R. J.; Tricker, B. J. K. (1969): Colonisation and extinction: the mice of Foula, with notes on those on Fair Isle and St. Kilda. J. Zool. (London) **158**, 247 -265.

Breise, L. A.; Smith, M. H. (1973): Competition between *Mus musculus* and *Peromyscus polionotus*. J. Mammalogy **54**, 968–969.

De Long, K. T. (1966): Population ecology of feral house mice: interference by *Microtus*. *Ecology* **47**, 481–484.

Doncaster, C. P. (1992): Testing the role of intraguild predation in regulating hedgehog populations. Proc. Royal Soc. Series B **249**, 113–117.

Dueser, R. D.; Porter, J. H. (1986): Habitat use by insular small mammals: relative effects of competition and habitat structure. Ecology **67**, 195–201.

Ebenhard, T. (1991): Colonisation in metapopulations: a review of theory and observations. Biol. J. Linnean Soc. **42**, 105–121.

Fitzgerald, B. M.; Karl, B. J.; Moller, H. (1981): Spatial organisation and ecology of a sparse population of house mice (*Mus musculus*). J. Animal Ecol. **50**, 489–518.

Fox, M. D.; Fox, B. J. (1986): The susceptibility of natural communities to invasion. In: Ecology of biological invasions. Ed. by R. H. Groves and J. J. Burdon. Cambridge: Camb. Univ. Press. Pp. 57–66.

Fox, B. J.; Gullick, G. (1989): Interspecific competition between mice: a reciprocal field manipulation experiment. Austral. J. Ecol. **14**, 357–366.

Fox, M. D.; Pople, A. (1984): Experimental confirmation of interspecific competition between native and introduced mice. Austral. J. Ecol. **9**, 323–334.

Granjon, L.; Cheylan, G. (1988): Méchanisms de coexistance dans une guilde de muridés insulaires (*Rattus rattus* L., *Apodemus sylvaticus* L. et *Mus musculus domesticus* Rutty) en Corse: conséquences évolutives. Z. Säugetierkunde **53**, 301–316.

King, C. M. (1982): Age structure and reproduction in feral New Zealand populations of the house mouse (*Mus musculus*) in relation to seedfall of southern beech (*Nothofagus*). New Zeal. J. Zool. **9**, 467–480.

Lidicker, W. Z. (1966): Ecological observations on a feral house mouse population declining to extinction. Ecol. Monogr. **36**, 27–50.

Lidicker, W. Z. (1976): Social behaviour and density regulation in house mice living in large enclosures. J. Animal Ecol. **45**, 677–697.

Lima, S. L.; Dill, L. M. (1990): Behavioral decisions made under the risk of predation: a review and prospectus. Can. J. Zool. **68**, 619–640.

Meehan, A. P. (1984): Rats and mice. Their biology and control. East Grinstead, UK: Rentokil.

Pelikán, J. (1981): Patterns of reproduction in the house mouse. Symp. Zool. Soc. London **47**, 205–229.

Stickel, L. F. (1979): Population ecology of house mice in unstable habitats. J. Animal Ecol. **48**, 871–887.

Walkowa, W.; Adamkzyk, K.; Chelkowska, H. (1989): Characteristics of migrants in a free-living population of the house mouse. Acta Theriol. **34**, 305–313.

Walkowa, W. (1981): Structure, dynamics and production of house mouse populations: a review of studies conducted at the Institute of Ecology, Polish Academy of Science. Symp. Zool. Soc. London **47**, 427–437.

Authors' addresses: Françoise H. Tattersall, Royal Agricultural College, Cirencester, Gloucestershire, GL7 6JS; R. H. Smith, School of Biological Sciences, University of Leicester, University Road, Leicester, LE1 7RH, and F. Nowell, School of Animal and Microbial Sciences, University of Reading, PO Box 228, Reading RG6 2AJ.

Z. Säugetierkunde **62** (1997) 359–371

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Quantitative investigation of the intestines in eight species of domestic mammals

By R. L. Snipes and Heidi Snipes

Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität Giessen, Giessen, FRG

Receipt of Ms. 02. 09. 1996
Acceptance of Ms. 18. 03. 1997

Abstract

Eight species of domestic mammals (dog, cat, horse, pig, cow, goat, sheep, and rabbit) were investigated using quantitative morphometric techniques to determine various functional parameters of the intestines. In addition to lengths and volumes, basal areas were measured directly on the entire large intestines. Histological sections were made from disc-shaped probes punched from predetermined areas of the intestine in order to calculate a factor of increase of the intestinal mucosa due to macroscopically and microscopically visible structures such as folds, mounds, villi, and crypts. Ratios of large intestine to small intestine for the parameters areas and volume as well as area to volume relationships were determined. According to this type of data handling, nonruminant herbivores are set apart from a collective taxonomically unrelated group including faunivores and intermediate feeders plus ruminant herbivores. This latter grouping is discussed in relation to their diet and large intestinal morphology.

Introduction

The availability of morphometric data on the intestines of domestic mammals is surprisingly dearth despite their obvious economic importance. Most data in textbooks are concerned with volumes (Slijper 1946; Flindt 1985) or lengths (Ellenberger and Baum 1943) and the latter are based largely on non-reproducible measurements that are 50 years and older. Although length is the most frequently measured parameter for intestine, it is not necessarily a reliable measurement or is it functionally the most important factor in the intestine. Far more interesting from the functional point of view is the surface area available for absorption and secretion in the various compartments of the intestine. The few data for areas available, for example presented by Chivers and Hladik (1980) from an extensive and heroic compilation of intestinal values for hundreds of species, were largely obtained by extrapolating areas from products of measured lengths times widths. This procedure may well be justifiable for animals whose intestines are uniform throughout their lengths, such as rodent small intestines (Young Owl 1994), however, it does not appear appropriate for large and voluminous intestines. Moreover, intestinal structures such as the spiral fold of the rabbit caecum or the plicae intestinales of the human small intestine, both of which add, respectively, 30 to 50% more surface area over and above the basal surface areas (Snipes 1996), are missed and ignored by such a procedure.

In all methods used to date, only few have taken into account the increase in surface area due to microscopically visible structures such as folds, crypts or villi. Therefore, it

was deemed expedient to employ a newly developed quantitative technique (Snipes and Kriete 1991) to obtain data from domestic animals. The technique should include the advantages of 1) measuring the entire large intestine even for such huge animals as horse or cow and thereby avoiding the obvious disadvantages of sampling and extrapolation, 2) including in these measurements any macroscopically visible and extractable structures (e. g. spiral fold of rabbit caecum) which increases the basal surface area, 3) determining a factor of surface enlargement due to microscopically measurable structures (villi, crypt, folds) and subsequently with this factor, 4) determining a total surface area as the product of the basal area times the microscopic surface enlargement factor.

Material and methods

Three animals each were used in the present study for reasons recently discussed by Snipes (1996). The domestic mammals investigated in the present study include:

dog: *Canis lupus* Linnaeus, 1758
cat: *Felix silvestris* Schreiber, 1777
horse: *Equus przewalskii* Poliakow, 1881
pig: *Sus scrofa* Linnaeus, 1758
cow: *Bos primigenius* Bojanus, 1827
goat: *Capra aegagrus* Erxleben, 1777
sheep: *Ovis ammon* Linnaeus, 1758
rabbit: *Oryctolagus cuniculus* Linnaeus, 1758.
(Nomenclature according to Herre and Röhrs 1990).

Rabbit, dog, and cat were obtained from veterinary physicians practicing all legal forms of euthanasia. Larger animals were obtained from the local abattoir. For the former animals, 4% buffered formol was injected into the lumen of the intestines immediately after death (Fenwick and Kruckenberg 1987). For the latter animals whole intestines were obtained as quickly as possible, opened and flooded with fixative. A thorough discussion of the effects of fixation and each step in the processing of material including reference to possible shrinkage can be found in Snipes (1996, 1997).

A standard methodology for determination of the basal surface areas of the various compartments of the intestines has been described in detail elsewhere (Snipes 1991; Snipes and Kriete 1991; Snipes 1994, 1996). For all animals the entire intestines were measured after having been opened lengthwise and probed for light microscopy (see below). The measurement consisted of tracing contours onto transparent paper of appropriately sized slabs of intestine placed between two glass plates. The contours were subsequently measured for areas (mm^2) using a software especially developed for this purpose and performed on a Kontron semiautomatic imagine analyser (Snipes and Kriete 1991). This procedure gave the basal areas of the tubular or saccular intestinal compartments (small intestine, caecum, colon) and was based on measuring the entire intestine.

To determine an additional increase in the mucosal surface area due to microscopically visible structures, probes were excised according to methods in works cited above. These were processed for light microscopy, the final sections projected via a slide projector onto a digitized tablet for measurement of the factor of increase in surface area due to crypts, villi, and folds. The length of the mucosa surface displaying these surface enlargements was traced with the cursor. This length was set in a ratio to a second length, a straight reference line drawn beneath the mucosal surface to give a Surface Enlargement Factor (SEF), which could then be multiplied times the basal areas to give a final total surface enlargement.

The histological probes were extracted from the small animals (rabbit, cat, dog) according to a scheme developed previously (Snipes and Kriete 1991). This consisted of three areas of the caecum (apex, corpus, caecocolical ampulla) and five equidistant areas of the colon. The probes were punched out with a cork borer, including at least 3/4 the circumference of the intestine. For the remainder of the animals (sheep, goat, pig, cow, horse) this procedure was not appropriate. The histological probes were taken according to a scheme such that the caecum/colon was divided into 20 equidistant lengths. Likewise, the opened intestinal circumference was divided into 20 equivalent sectors. Probes were then extracted with the largest cork borer according to the following protocol. Probe 1 was taken from length # 1 and circumferential sector # 1; probe 2 from length # 2 and circumferential sector # 2 etc. All probes

were taken as discs and embedded according to the principle of vertical sectioning (Baddley et al. 1986). It should be noted here that all macroscopically visible structures such as folds or plicae were excised with scissors and measured as a part of the basal area.

Using this protocol it was felt that an optimal measurement was carried out: for the basal area the entire intestine and for the microscopic surface enlargement factor determination, large probes according to predetermined sampling sites.

Results

In table 1 the lengths and volumes of small intestine, caecum, colon and the total of these three regions are presented according to increasing body weight. The percentage of each parameter to the total is also given. Volumes were calculated from the measured areas. For all species, small intestines represent over 50% of the total intestinal length. For volume, the caecum and colon of rabbit and horse account for a greater percentage than small intestine.

Table 1. Morphometric values, length and volume.
Measured lengths and the percentage of each compartment to total intestinal length. Species name and body weights in kg given for the eight species studied, listed according to increasing body weight. Calculated values of volume in ml and their percentage to total volume of intestine for small intestine, caecum, colon, and total intestine. sm int = small intestine

Species Body Weights kg	Length cm				Volumes ml			
	sm. int	caecum	colon	total	sm. int	caecum	colon	total
Rabbit (*Oryctolagus cuniculus*) 3.6	196.3 55.9%	40.7 11.6%	114.2 32.5%	351.2	79.3 12.3%	514.2 79.9%	50.1 7.8%	643.6
Cat (*Felis silvestris*) 3.7	148.3 86%	2.0 1%	22.3 13%	172.5	48.3 77.8%	2.9 4.7%	10.9 17.6%	62.1
Dog (*Canis lupus*) 13.6	270 86.5%	42 13.5%	75 24%	312	373 70.7%	34.5 6.5%	120 22.7%	527.5
Sheep (*Ovis ammon*) 42.5	2 153 77%	25 0.9%	615 22%	2 793	1 503 59%	284 11%	766 30%	2 553
Goat (*Capra aegagrus*) 52.5	953 68.4%	21 1.5%	420 30.1%	1 394	1 187 71.1%	1 140.6 8.4%	340.9 20.4%	1 668.5
Pig (*Sus scrofa*) 111.9	1 823.3 74%	28.2 1.2%	610.7 24.8%	2 462.2	4 406.6 50.2%	564.8 6.4%	3 808.1 43.4%	8 779.5
Cow (*Bos primigenius*) 474.3	4 073.3 80.1%	57 1.1%	954.7 18.8%	5 085	14 662.8 72.9%	857.7 4.3%	4 598.8 22.9%	20 119.3
Horse (*Equus przewalskii*) 520.0	3 020 77.8%	120 3.1%	740 19.1%	3 880	46 897.3 25.1%	56 083 30%	83 892.7 44.9%	186 873

Table 2. Morphometric values, areas.
Basal areas, second order enlargement factor (SEF) and total areas for small intestine, caecum, colon, and total intestine for the 8 species studied, listed according to increasing body weights. Percents give the proportion of each segment to total intestinal values. Total areas were arrived at by multiplying basal areas times SEF factor.

Species Body Weight kg	Basal Area				SEF			Total Area			
	sm. int cm^2	caec cm^2	colon cm^2	total cm^2	sm. int	caec	colon	sm. int cm^2	caecum cm^2	colon cm^2	total cm^2
Rabbit (*Oryctolagus cuniculus*) 3.6	442.2 36.2%	512.5 41.9%	268.1 21.9%	1 222.8	3.50	2.18	1.80	1 548.1 49.1%	1 121.1 35.5%	485.2 15.4%	3 154.4
Cat (*Felis silvestris*) 3.7	300 75.6%	8.5 2.1%	88.4 22.3%	396.8	5.97	1.71	1.68	1 791 91.7%	14.5 0.7%	148.5 7.6%	1 954
Dog (*Canis lupus*) 13.6	1 124.8 78.4%	57.7 3.9%	251.6 17.5%	1 434.1	4.04	1.63	1.70	4 544.2 89.7%	94.1 1.9%	427.7 8.4%	5 066.0
Sheep (*Ovis ammon*) 42.5	6 377.4 70.0%	298.9 3.3%	2 433.6 26.7%	9 109.9	2.81	1.69	1.75	17 920.5 79.0%	505.1 2.2%	4 258.8 18.8%	22 684.4
Goat (*Capra aegagrus*) 52.5	3 770.3 71.1%	192.6 3.6%	1 341.2 25.3%	5 304.1	1.30	1.20	1.18	4 901.4 73.0%	231.1 3.4%	1 582.6 23.6%	6 715.1
Pig (*Sus scrofa*) 111.9	10 047.3 63.0%	447.0 3.0%	5 405.3 34.0%	15 899.6	3.36	2.59	2.35	33 758.9 70.9%	1 157.7 2.4%	12 702.5 26.7%	47 619.1
Cow (*Bos primigenius*) 474.3	27 393.5 76.9%	783.8 2.2%	7 426.9 20.9%	35 604.2	2.80	1.44	1.60	76 701.8 85.5%	1 128.7 1.3%	11 883.0 13.2%	89 713.5
Horse (*Equus przewalskii*) 520.0	42 183.4 53.2%	9 195.4 11.6%	27 928.1 35.2%	79 306.9	2.45	1.32	1.46	103 349.3 66.1%	12 137.9 7.8%	40 775 26.1%	156 262.2

In table 2 the species are again listed according to increasing body weights for basal areas, the surface enlargement factor (SEF) determined by measuring the histological sections, and the total area as the product of the basal area times SEF. Percents of areas are also given. For areas, only the rabbit caecum plus colon has a larger surface area than the small intestine. In all other species, including horse the area of the small intestine, as primary intestinal segment for absorption of nutrient, possesses the most extensive mucosal surface.

Table 3 presents some simple handling of the data to illustrate more clearly the relationships of certain areas of the gut to one another. The coefficient of digestion (according to Chivers and Hladik 1980) is a ratio resulting from dividing the basal area or total area of the large intestine by the corresponding value of the small intestine. These values give an estimation of the functional importance of the large intestine in the utilization of the diet. These ratios are multiplied by 100 and scaled according to a scheme developed by Chivers and Hladik (1980, 1984) such that values between 0–30 are considered faunivores (and newly determined in the present study also ruminants), 30–70 as intermediate feeders and +70 as nonruminant herbivores. From the present data rabbit and horse qualify as nonruminant herbivores as regards basal area, only rabbit regarding total area. Pig ranges with its value of 58 (basal) and 41 (total area) as intermediate feeder together with goat (41 and 37, respectively) as well as horse for total area (51), sheep and cat for basal area (43 and 32, respectively). All other species qualify as faunivores or ruminants (values below 30). Amongst all ruminants the goat has the largest hindgut (Hofmann 1991).

Table 3. Coefficient of Gut Differentiation.
Coefficient of Gut Differentiation (Coef Dig) = Areas of large intestine divided by areas of small intestine. According to Chiver and Hladik (1980, 1984) a scale was devised dividing animals (but not considering the ruminants) roughly into three dietary groups (faunivores, intermediate feeders and herbivores). At left calculations using basal areas, at right calculations using total areas. All values ×100. Ratings: faunivores = 0–30; intermediate feeders = 30–70, and nonruminant herbivores above a value of 70. Note that values for ruminants fall either in the faunivore or intermediate feeder ranges.

Coefficient of Gut Differentiation Areas Large Intestine/Areas Small Intestine				
Animals	Basal Area	Rating	Total Area	Rating
Dog	27	Faunivore	1.5	Faunivore
Cow	3	Ruminant	17	Ruminant
Cat	32	Faunivore/Intermediate	9	Faunivore
Goat	41	Ruminant	37	Ruminant
Sheep	43	Ruminant	27	Ruminant
Pig	58	Intermediate	41	Intermediate
Horse	88	Herbivore	51	Intermediate
Rabbit	177	Herbivore	104	Herbivore

The Coefficient of Volume (Tab. 4) is a similar ratio but uses volumes of large and small intestine. Values are multiplied by 10 according to Chivers and Hladik (1980) and scaled accordingly: 0–7 = faunivore (or as ruminants as determined newly in this study), 7–15 = intermediate feeders; and +15 = nonruminant herbivores. According to this status, again rabbit and horse qualify as nonruminant herbivores. All other animals examined range as faunivore or ruminant except for pig (9.9) as intermediate feeder. Values for

Table 4. Coefficient of Volume.
Coefficient of Volume = Volumes of large intestine divided by volumes of small intestine. Ratings divide the animals roughly into three dietary groups (originally excluding ruminant): faunivores (0–7), intermediate feeders (7–15) and nonruminant herbivores (above 15). All values multiplied by 10. Ratings according to Chivers and Hladik (1980, 1984). Ruminants show values in the faunivore range. Note that stomach and in the case of ruminants the fore-stomach were not included in the calculations.

Coefficient of Volume Volume Large Intestine/Volume Small Intestine			
Ruminant Rating: 0–7	Faunivore Rating: 0–7	Intermediate Rating: 7–15	Nonruminant Herbivore Rating: +15
Cow 3.7	Cat 2.9	Pig 9.9	Horse 29.8
Goat 4.1	Dog 4.1		Rabbit 71.2
Sheep 7.0			

goat are borderline between intermediate and ruminant (7.0, see explanation above). The nomination according to the classical three dietary types: faunivore (carnivore), intermediate (omnivore) and nonruminant herbivore given by Chivers and Hladik (1980) must now be altered such that values for faunivores are shared by the ruminants.

Another helpful mode of handling data represents the use of area to volume ratios (Tab. 5). This relative area designation illustrates the functionally important relationship of the potential contact of luminal content to the surface mucosa. In table 5 these values are given for small intestine, caecum, colon, and total intestine for relative basal area to volume and relative total area to volume. Large values represent a favourable relationship of area to volume. In this case a tendency for higher values to occur in the smaller animals (body weights) compared to large animals is apparent.

Table 5. Relative areas (areas to volume ratios).
Area to Volume Ratios = Areas of small intestine, caecum and colon divided by their respective volumes. Smaller animals have larger values commensurate with their higher metabolic rates reflecting a more advantageous area to volume relationship. For each region of the intestine (small, caecum and colon as well as total intestine) values using basal areas and total areas are given. Animals are listing according to increasing body weights.

Area (cm^2) to Volume (ml)								
Animals + body weights kg	Small intestine		Caecum		Colon		Total Intestine	
	Basal	Total	Basal	Total	Basal	Total	Basal	Total
Rabbit 3.6	5.8	19.5	1.0	2.2	5.3	9.7	1.9	4.9
Cat 3.7	6.2	37.1	2.9	5.0	8.1	13.6	6.4	31.5
Dog 13.6	3.0	18.0	1.7	2.9	2.1	3.5	2.7	13.7
Sheep 42.5	4.2	11.9	1.1	1.8	3.2	5.6	3.6	8.9
Goat 52.5	3.2	4.1	1.4	1.6	3.9	4.6	3.2	4.0
Pig 111.9	2.3	7.6	0.8	2.0	1.4	3.3	1.8	5.4
Cow 474.3	1.9	5.2	0.9	1.3	1.6	2.6	1.8	4.5
Horse 520.0	0.9	2.2	0.2	0.2	0.3	0.5	0.4	0.8

Table 6. Comparative Percentage Values.
Values from the literature (source given in small print beneath each animal name) converted to percentages of each compartment (small intestine, caecum, colon) to total intestine for the parameters basal area and volume compared to values obtained in the present study.

Animal	Basal area %			Volume %		
Source	small int.	caecum	colon	small int.	caecum	colon
Rabbit						
Chivers and Hladik (1980)	50%	27.6%	22.5%	31.3%	51.6%	17.1%
Neumayer (1990)				71.5%	28.5%	
Flindt (1985)				44.4%	37%	18.6%
present study	36.2%	41.9%	21.9%	12.3%	79.9%	7.8%
Cat						
Chivers and Hladik (1980)	71.7%	2.0%	26.3%	57.3%	2.0%	40.7%
Custor (1873)	68.4%	31.6%				
present study	75.6%	2.1 %	22.5%	77.8%	4.7%	17.6%
Dog						
Chivers and Hladik (1980)	82.4%	2.9%	14.7%	77.5%	3.6%	18.9%
Custor (1873)	79.9%	20.1%				
Neumayer (1990)				71.5%	28.5%	
Flindt (1985)				61.8%	3.4%	34.7%
present study	78.4%	3.9%	17.5%	70.7%	6.5%	22.7%
Sheep						
Chivers and Hladik (1980)	79.9%	2.3%	17.9%	77.4%	6.4%	16.2%
Custor (1873)	60.3%	39.7%				
Ellenberger and Baum (1943)					10.0%	
Flindt (1985)				61.6%	6.9%	31.4%
present study	70.0%	3.3%	26.7%	59.0%	11.0%	30.0%
Goat						
Chivers and Hladik (1980)	66.9%	2.5%	30.6%	56.4%	5.6%	38.0%
Custor (1873)	58.8	41.2%				
Flindt (1985)				61.6%	6.9%	31.4%
present study	71.1%	3.6%	25.3%	71.1%	8.4%	20.4
Pig						
Chivers and Hladik (1980)	67.4%	2.6%	30.0%	55.0%	5.6%	39.3%
Slijper (1946)	63.7%	4.4%	31.9%	46.2%	5.1%	48.7%
Custor (1873)	64.8%	35.2%				
Flindt (1985)				47.3%	7.9%	44.8%
present study	63.0%	3.0%	34.0%	50.2%	6.4%	43.4%

Table 6. (Continued)

Animal	Basal area %			Volume %		
Source	small int.	caecum	colon	small int.	caecum	colon
Cow						
Slijper (1946)	69.5%	5.7%	24.8%	63.5%	9.5%	26.9%
Ellenberger and Baum (1943)					13.1%	29.2%
Flindt (1985)				63.4%	10.0%	27.1%
present study	76.9%	2.2%	20.9%	72.9%	4.3%	22.9%
Horse						
Chivers and Hladik (1980)	22.8%	19.2%	58.0%	7.3%	33.3%	59.4%
Slijper (1946)	38.0%	13.0%	49.0%	30.9%	20.5%	48.6%
Ellenberger and Baum (1943)				35.3%	16.7%	47.9%
Flindt (1985)				33.0%	17.4%	49.6%
present study	53.2%	11.6%	35.3%	25.1%	30.0%	44.9%

In table 6 data from four different sources were compared with data from the present study. It was necessary to convert and conform these data into percentages so that a comparative basis could be created. As stated previously, the functionally important parameters are considered to be area and volume. Although lengths of intestines have in the past been more commonly compiled these are considered to be of lesser relevance functionally.

Discussion

The large intestine of ruminants has been largely ignored in the literature except for a few interesting reviews (e. g. Janis 1976; Sibly 1981; Hofmann 1989, 1991), most probably due to the prominence and importance of the rumen-reticulum. It is interesting to note in the present study that values measured for most of the ruminants fall into categories with faunivores. The categorisations should not be taken as necessarily showing functionally similar utilization of diets in these cases but rather that in both ruminants and faunivores the large intestine plays a lesser functionally important role compared to nonruminant herbivores and intermediate feeders.

Comparison with data in the literature is rendered extremely difficult due to the lack of uniformity in the mode of obtaining the data and the handling of the data. Despite this lack of uniformity of data in the literature an attempt at comparing the few compilations available was undertaken. It can be seen that most of the values from different authors range relatively close together. The present values for rabbit, however, differ from previous studies. This is most likely due to the fact that in our study we considered the basal area due to the spiral fold in the caecum of the rabbit which previous authors ignored. This fold accounts for up to 53% of the area in the caecum (Snipes 1996). This most certainly accounts for the difference in the values for rabbit and emphasizes the importance of careful consideration of the structures to be selected for measurement.

The present values for the horse are also slightly divergent from those of previous authors with respect to the proportion due to small intestine. The volumes of large intes-

tine are all very close (44 to 49%). The percentages of area and volume for the large intestine for both horse and rabbit are the highest amongst the studied animals as would be expected for nonruminant herbivores. Only the pig (as true intermediate feeder) possesses values for colon that approach those for the two afore-mentioned animals. All other listed animals, the faunivores (cat and dog) and the ruminants (sheep, goat, and cow) have lower values for percentages of the large intestine.

The only other complete source of data for comparative purposes is that of CHIVERS and HLADIK (1980, 1984). In addition to measured values, we have emphasized the relative proportions or the use of coefficients. Coefficients for total areas include the second-order enlargements of the surface area due to such structures as crypts, microscopic folds, and villi. This form of categorisation shows that such structures are more highly developed in the large intestines of nonruminant herbivores (larger values for rabbit and horse), which correlates with their voluminous macroscopic forms. Ruminants and faunivores have lower values emphasizing the greater functional importance of the intestinal compartments oral to the large intestines. Coefficients of volume are also higher in the two nonruminant herbivores reflecting the fermentation chamber function of their caecum plus colon compartments.

The relative surface area related to volume displays a general tendency for animals with smaller body weights to possess higher values, indicative of a more advantageous mucosal surface area relationship to luminal content, which may be more effective for rapid absorption of nutrients. This has been interpreted as reflecting the higher energy requirements of metabolically more active smaller animals (KARASOV and DIAMOND 1985; SNIPES 1996). In a previous study (SNIPES and KRIETE 1991) comparing 19 different mammalian species this tendency was even more obvious. This weight-dependent association is more apparent using a larger sample of animals of wider weight ranges. This can be visualized to better advantage via linear regression curves (and a wider range of animals) which correlate closely to metabolic body weights (SNIPES 1996).

The fact that herbivores whose fermenation chambers are set before the large intestine (ruminants) can be grouped with faunivores based on morphometric parameters is upon initial consideration perhaps a surprising finding, and may even seem contradictory. However, this grouping is a consequence of the functional importance of that portion of the intestinal tract lying proximal to the ileocaecal junction, be it the rumen-reticulum in ruminants or the small intestine in faunivores. This finding is corroborated by several physiological data.

Since the enzyme machinery to breakdown cellulose is missing in many vertebrates, the nutrient value of its breakdown products as well as the cellular contents are deprived to the host animal. Two morpho-physiological modes of coping with this problem were evolved, namely, the development of a fermentation chamber for the breakdown of cellulose via bacteria set before the small intestine (foregut fermenters, ruminants) or distal to the small intestine (so-called hindgut fermenters or better caecal or caecocolical fermenters; HUME and WARNER 1980). The obvious advantage of the former is that the breakdown products can be readily digested and absorbed as they pass into the small intestine which lies in direct sequence to the foregut-fermenting chamber. In order for the latter mode to be effective where the fermentation chamber is aboral to the major site of absorption the animals should have to ingest their own faeces, a process known as coprophagy. A special form of coprophagy observed especially in lagomorphs is caecotrophy, ingestion of specially formed faecal pellets directly from the anus usually nocturnally (HÖRNICKE and BJÖRNHAG 1980). Hereby, the nutrients broken down in the large intestine and now held within the pellets are exposed to the small intestine “a second time around” and can be digested and absorbed. Another alternative would be actual absorption in the large intestine itself. Although the small intestine is the major site of absorption in all animals regardless of dietary type some animals indeed do depend largely on absorption in

their large intestines; rabbits account for up to 30% of their energy needs via this route (Parker 1976); in sheep between 4.2% and 26% of digestible energy is accountable by digestion in the large intestine (Ulyatt et al. 1975). Also in pigs, 9.6% to 11.6% of energy requirements depending on carbohydrate diet results from volatile fatty acid production and absorption in the large intestine (Imoto and Namioka 1978). Thus, both hindgut fermenters as well as ruminant forms and intermediate feeders all rely on the fermentation function of their caecum and proximal colon.

Both ruminants and hindgut fermenters use a very similar approach to utilize plant cell walls and cellular content not available to the animals' own hydrolytic enzymes. In both fermentation systems the main end products of ATP-yielding catabolism are volatile fatty acids and microbial biomass (Demeyer and de Graeve 1991), the slight difference being the prominence of methanogenesis in ruminants and acetogenesis in hindgut fermenters.

The major advantages and disadvantages as well as limitations of the two modes of dietary utilization have been established in various comprehensive surveys (e. g. Janis 1976; Hofmann 1989, 1991), size being one limitation (size range for ruminants being between 5 to 1 600 kg) and diet content another (high fibre content can only be tolerated by the ruminant to a certain limit). Here, caecal fermentation becomes advantageous when dealing with high fibre content food, provided intake is not limited (Janis 1976). The larger the herbivore the more fibrous the diet can be. The larger animals have lower energy requirements and thus can tolerate more fibre in their diets. Recent small-sized herbivores are almost all hindgut fermenters (hydraces, rodents, lagomorphs) but usually have developed special dietary adaptations such as eating their own faeces (Hörnicke and Björnhag 1980).

In faunivores (dog and cat), the primary functional role of the large intestine is the aboral transport of undigested nutrient and the absorption of water and electrolytes. The latter function is also a prominent function in all mammals (Höller et al. 1988; Leng 1978; Vernay 1986; Olszewski and Buraczeski 1978).

Through specialization in some species of their selection of nutrient the large intestine has increased in size and differentiation (rabbit, horse). The large intestine has gained an important role in the total digestive process of these animals. In other animals the large intestine has a lesser importance, as in faunivores and ruminants (Drochner and Meyer 1991), at least during normal species-specific nutrition. Accordingly, the percent of total digestibility located in the large intestine for organic substances is lowest for dog and ruminants (both 8%) and highest for horse (25%), and intermediate for pig (17%) (Drochner and Meyer 1991).

The amount of postileal digestion of organic matter depends not only on the species but also the type of food. By feeding pigs and dogs foodstuffs of low digestibility, the postileal digestion increased to 50% and 24%, respecitvely (Kim et al. 1978; Drochner and Meyer 1991).

Other nutrient and physiological similarities of faunivores and ruminants are their crude fibre fermentation (carnivores 7%, ruminants 16%) compared to pigs (17% to 43%) and horses (32%–52%). Degradation of nitrogenous compounds in the large intestine varies from 20% in ruminants to 50% in horses. Net absorption of N/kg body mass$^{0.75}$/day equals 0.1 mg in ruminants and carnivores, and 0.16 mg in pigs, 0.2 mg in horses (Drochner and Meyer 1991; Olszweski and Buraczewski 1978; Niiyama et al. 1979). Thus, microbial digestion in the large intestine in all species serves additional energy supply. Although of lesser differentiation than most large intestines of hindgut fermenters, the caecum of most ruminants is larger and more voluminous than expected (Hofmann 1991). Perhaps the answer to this can be found in the above-mentioned physiological fact that the large intestine of ruminants plays a role in digesting products that have escaped digestion in the forestomach and absorption in the small intestine. This is especially important when overall digestibility decreases.

The present results of a loose grouping of faunivores with ruminants are in compliance with the above-mentioned physiological data. Indeed the present morphometric data simply reflect a predominance of the structural-functional parameters in the large intestine of the hingut nonruminant fermenter compared to the ruminants whose fermentation occurs further orally and faunivores whose selective proteinaceous diets exludes the necessity of a well-developed hindgut fermentative function. This does not, however, exclude the possibility of fermentation taking place in such animals with a greater structural-functional emphasis in the small intestines, like dog, cat, and human. The morphometric parameters for the latter species are such that they also group with faunivores (SNIPES 1996). The human large intestine resembles structurally the large intestine of a hindgut fermenter (taeniae, haustra, semilunar folds) as well as possesses resident bacteria and displays production of volatile fatty acids (BUSTOS FERNÁNDEZ 1983). However, in the case of humans, the small intestine has undergone an enormous structural differentiation, especially in its surface enlargement due to the presence of the plicae circulares (SNIPES 1996, 1997). This emphasis in favour of the small intestine which is reflected in the morphometric parameters obscurs the purely structural aspects of the large intestine resembling hindgut fermenting forms. This emphasizes the importance of coordinating morphometrical studies with morphological observation.

Thus, although structurally very different, the large intestines of ruminants and faunivores display morphometric parameters that allow them to be classified together. These data expressed in the form of coefficients and ratios reflect solely the proportion and the importance of small intestine in the carnivore and ruminant, and the relative lesser importance of the large intestine in the utilization of their dietary regime. This is the foundation of the similarity and reason for being able to be classified together. The nomenclature for the coefficients adopted from CHIVERS and colleagues (CHIVERS and HLADIK 1980) is perhaps now misleading (i. e. faunivore now together with ruminant herbivores; omnivores now called intermediate feeders; and herbivores actually meaning only nonruminant herbivores). In their studies ruminants were not included. For the first time then ruminants have been considered under such a categorisation. The terms coefficient of digestion and fermentation express physiological processes, although being determined by morphometrically measurable parameters. Perhaps the latter would more appropriately be termed Coefficient of Relative Volume as practised in the present study (SNIPES and KRIETE 1991), the former Coefficient of Surface Area. Categorisation is merely an attempt to bring some order into a mass of measurements. It must not be seen as a strigent restrictive grouping but rather as a continuum between two extremes for better visualisation of comparative aspects.

Acknowledgements

The authors thank STEPHAN WÖBBEKING, HEIDRUN SUST, and the late FRANK LUTZ for help in obtaining material from large animals and preliminary handling of some material. Prof. Dr. P. LANGER (Giessen) gave excellent constructive criticism during preparation of the manuscript for which we are greatly appreciative.Thanks are also due to Prof. Dr. Dr. H.-R. DUNCKER (Giessen) for encouragement and enabling this work to be accomplished.

Zusammenfassung

Quantitative Untersuchung an Därmen von acht verschiedenen Haustierarten

Acht verschiedene Haustierarten (Hund, Katze, Pferd, Schwein, Kuh, Ziege, Schaf und Kaninchen), wurden mit quantitativen morphometrischen Methoden untersucht um verschiedene funktionelle Parameter des Darmes zu erläutern. Zusätzlich zu Länge und Volumen, wurden die Grundfläche des gesamten Darmes gemessen. Histologische Schnitte von scheibenförmigen Proben, die aus vorbestimmten

Bereichen des Darmes gestanzt wurden, dienten zur Bestimmung eines Faktors der Zunahme der Darmoberfläche, die durch Falten, Zotten oder Krypten hervorgerufen sind. Aus den morphometrisch gewonnenen Daten wurde der sogenannte Koeffizient der Verdaulichkeit bzw. der Koeffizient der Fermentation bestimmt. Das Verhältnis Fläche zu Volumen als funktionell wichtige Parameter wurde ebenfalls bestimmt. Werte für Ruminantia fallen in die gleiche Kategorie wie für Faunivoren. Kaninchen und Pferd zeigen Werte, die für Herbivoren charakteristisch sind. Alle anderen untersuchten Tierarten gelten als Faunivoren oder Ruminantia. Das Verhältnis Fläche zu Volumen zeigt die Tendenz, daß kleinere Tiere höhere Werte besitzen (Kaninchen, Katze, Hund).

References

BADDLEY, A. J.; GUNDERSEN H. J. G.; CRUZ-ORIVET, L. M. (1986): Estimation of surface area from vertical sections. J. Microscopy **142**, 259–276.

BUSTOS-FERNÁNDEZ, L. (1983) Colon. Structure and Function. New York London: Planum Med Book Co.

CHIVERS, D. J.; HLADIK, C. M. (1980): Morphology of the gastrointestinal tract in primates: comparisons with other mammals in relation to diet. J. Morphol. **166**, 337–386.

CHIVERS, D. J.; HLADIK, C. M. (1984): Diet and gut morphology. In: Food acquisition and processing in primates. Ed. by D. J. CHIVERS, B. A. WOOD and A. BILSBOROUGH. New York: Plenum Press. Pp. 213–230.

CUSTOR, J. (1873): Über die relative Grösse des Darmkanales und der hauptsächlichsten Körpersysteme beim Menschen und bei Wirbelthieren. Arch. Anat. Phys. **1873**, 478–504.

DEMEYER, D. I.; DE GRAEVE, K. (1991): Differences in stoichiometry between rumen and hindgut fermentation. In: Physiology of the Hindgut. Ed. by M. KIRCHGESSNER. Advances in Animals Physiology and Animal Nutrition. Suppl. to J. Anim. Nutr. **22**, 50–61.

DROCHNER, W.; MEYER, H. (1991): Verdauung organischer Substanzen im Dickdarm verschiedener Haustierarten. In: Physiology of the Hindgut. Ed. by M. KIRCHGESSNER. Advances in Animals Physiology and Animal Nutrition. Suppl. to J. Anim. Nutr. **22**, 18–40.

ELLENBERGER-BAUM, (1943): Handbuch der vergleichenden Anatomie der Haustiere. 18. Auflage. Heidelberg: Springer Verlag. Pp. 400–401.

FENWICK, B. W.; KRUCKENBERG, S. (1987): Comparison of methods used to collect canine intestinal tissues for histologic examination. Am. J. Vet. Res. **48**, 1276–1281.

FLINDT, R. (1985): Biologie in Zahlen. Eine Datensammlung in Tabellen mit über 9000 Einzelwerten. Ernährung, Verdauung. Stuttgart: Gustav Fischer Verlag.

HERRE, W.; RÖHRS, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart: Gustav Fischer Verlag.

HOFMANN, R. R. (1989): Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologica **78**, 443–457.

HOFMANN, R. R. (1991): The comparative morphology and the functional adaptive differentiation of the large intestine of the domestic mammals. In: Digestive Physiology of the Hindgut. Ed. by M. KIRCHGESSNER. Advances in Animals Physiology and Animal Nutrition. Suppl. to J. Anim. Nutr. **22**, 7–17.

HÖLLER, H.; FIGGE, A.; RICHTER, J.; BREVES, G. (1989): Nettoresorption von Calcium und von anorganischem Phosphat aus dem perfundierten Colon und Rectum von Schafen. J. Anim. Physiol. Nutr. **59**, 9–15.

HÖRNICKE, H.; BJÖRNHAG, G. (1980): Coprophagy and related strategies for digesta utilization. In: Digestive Physiology and Metabolism in Ruminants. Ed. by Y. RUCKEBUSCH and P. THIVENS. Lancaster: MTP Press.

HUME, I.; WARNER, C. I. (1980): Evolution of microbial digestion in mammals. In: Digestive Physiology and Metabolism in Ruminants. Ed. by Y. RUCKEBUSCH and P. THIVENS. Lancaster: MTP Press.

IMOTO, S.; NAMIOKA, S. (1978): Volatile fatty acid production in the pig large intestine. J. Anim. Sci. **47**, 467–478.

JANIS, C. (1976): The evolutionary strategy of the Equidae and the origins of rumen and cecal digestion. Evolution **30**, 757–774.

KARASOV, W. H.; DIAMOND, J. M. (1985): Digestive adaptations for fueling the cost of enothermy. Science **228**, 202–204.

KIM, K.-I.; BENEVENGA, N. J.; GRUMMER, R. H. (1978): Lactase activity and volatile fatty acid production in the caecum and colon of pigs fed a corn-soy or 40% whey diet. J. Anim. Sci. **46**, 1648–1657.

LENG, E. (1978): Absorption of inorganic ions and volatile fatty acids in the rabbit caecum. Brit. J. Nutr. **40**, 509–519.

NEUMAYER, H. (1900): Über Capacität des Verdauungscanales. Sber. Jes. Morph. Physiol. München.

NIIYAMA, M.; DUGUCHI, E.; KAGOTA, K.; NAMIOKA, S. (1979): Appearance of 15N-labeled intestinal microbial amino acids in the venous blood of the pig colon. Am. J. Vet. Res. **40**, 716–718.

OLSZEWSKI, A.; BURACZEWSKI, S. (1978): Absorption of amino acids in isolated pig caecum in situ. Acta Physiol. Pol. **29**, 167–176.

PARKER, D. S. (1976): The measurement of production rates of volatile fatty acids in the caecum of the conscious rabbit. Br. J. Nutr. **36**, 61–70.

SIBLY, R. (1981): Strategies of digestion and defecation. In: Physiological Ecology. Ed. by C. R. TOWNSEND and P. CALLOW. Oxford: Blackwell Scientific Publ.

SLIJPER, E. J. (1946): Die physiologische Anatomie der Verdauungsorgane bei den Vertebraten. In: Tabulae Biologicae. Ed. by V. J. KONINGSBERGER, E. J. SLIJPER, and H. J. VONK. Amsterdam: W Junk.

SNIPES, R. L. (1991): Morphology of the mammalian cecum and colon. Microscopic and morphometric considerations. In: Hindgut '91. Ed. by T. SAKATA and R. L. SNIPES. Tokyo: Senshu University Press. Pp. 1–27.

SNIPES, R. L. (1994): Morphometric methods for determining surface enlargement at the microscopic level in the large intestine and their application. In: The Digestive System in Mammals. Ed. by D. CHIVERS and P. LANGER. Cambridge: Cambridge University Press. Pp. 234–263.

SNIPES, R. L. (1996): Morphometry of the mammalian intestinal system. A methodological concept to incorporate the functionally important structural parameters of intestinal absorptive surfaces. Habilitationsschrift. Fachbereich Humanmedizin der Justus-Liebig-Universität Giessen.

SNIPES, R. L. (1997): Intestinal Absorptive Surface in Mammals of Different Sizes. Adv. Anat. Embryol. Cell. Biol. Vol. 138 Heidelberg: Springer Verlag Pp. 1–88.

SNIPES, R. L.; KRIETE, A. (1991): Quantitative investigation of the area and volume in different compartments of the intestine of 18 mammalian species. Z. Säugetierkunde **56**, 225–244.

ULYATT, M. J.; DELLOW, D. W.; REID, C. S. W.; BAUCHOP, T. (1975): Structure and function of the large intestine of ruminants. In: Digestion and Metabolism in Ruminant. Armidale: Univ. of New England Publish Unit. Pp. 119–133.

VERNAY, M. (1986): Colonic absorption of inorganic ions and volatile fatty acids in the rabbit. Comp. Biochem. Physiol. **83 A**, 775–784.

YOUNG OWL, M. (1994): A direct method for measurement of gross surface area of mammalian gastrointestinal tracts. In: The Digestive System in Mammals. Ed. by D. CHIVERS and P. LANGER. Cambridge: Cambridge University Press. Pp. 219–233.

Authors's address: PD Dr. ROBERT L. SNIPES and HEIDI SNIPES, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität Giessen, Aulweg 123, D-35385 Giessen, Germany

Z. Säugetierkunde **62** (1997) 372–374

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

WISSENSCHAFTLICHE KURZMITTEILUNG

On the karyotype of the Long-eared hedgehog, *Hemiechinus auritus* (Gmelin, 1770) (Mammalia: Insectivora), in Turkey

By E. Çolak, N. Yiğit, M. Sözen, and Ş. Özkurt

Department of Biology, University of Ankara, Ankara and
Department of Biology, University of Gazi, Kırşehir, Turkey

Receipt of Ms. 16. 12. 1996
Acceptance of Ms. 09. 06. 1997

Hemiechinus auritus is distributed throughout Libya, Egypt, Israel, Lebanon, Syria, Turkey, USSR, Iran, Afghanistan, Pakistan, Mongolia, and China (Ellerman and Morrison-Scott 1951; Bobrinsky et al. 1965; Niethammer 1969; Harrison 1972; Corbet 1978, 1988; Osborn and Helmy 1980; Schoenfeld and Yom-Tov 1985; Harrison and Bates 1991). The karyotype of this species of hedgehog was described from Daghestan (Orlov 1969), Egypt (De Hondt 1972), Iraq (Bhatnagar and El-Azawi 1978), Afghanistan (Gropp et al. 1969), India (Sobti and Gill 1980), but not from other regions. The aim of the present study is to describe karyological characteristics of *H. auritus* in Turkey.

We collected 12 specimens from four localities (Fig. 1) (Aralyk 2, Ceylanpınar 3, Harran 5, Nizip 2) in Turkey and karyotyped four specimens from Ceylanpınar, Harran, and Nizip in southeastern Turkey. Karyotype preparations were made from bone narrow of animals treated with colchicine according to Ford and Hamerton (1956). 25 metaphase cells of each animal were examined.

H. auritus has 2 n = 48, NFa = 92 and NF = 96. All the autosomal pairs are bi-armed. The karyotype has a large submetacentric, a large subtelocentric pair, six dot-like chromo-

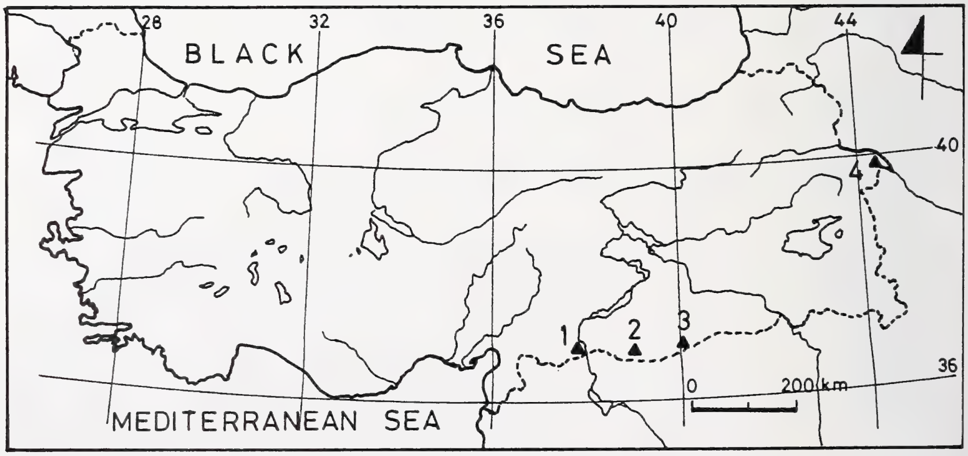


Fig. 1. Recorded localities (▲) of *H. auritus*. 1. Nizip, 2. Harran, 3. Ceylanpınar, 4. Aralyk

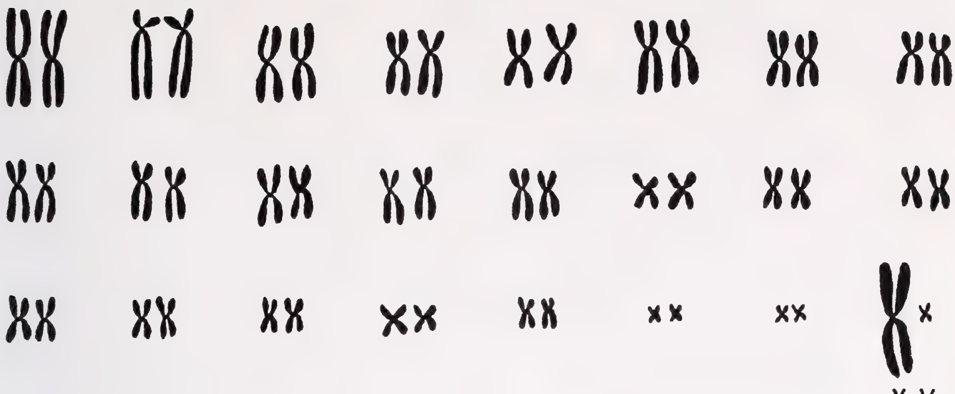


Fig. 2. The karyotype of a male *H. auritus* from Harran.

somes, and 18 pairs of submetacentric and metacentric ones. The X chromosome is a large metacentric and the Y chromosome is the smallest metacentric (Fig. 2).

The karyotype of *H. auritus* also contains 2 n = 48 chromosomes in Iraq (Bhatnagar and El-Azawi 1978), in Daghestan (Orlov 1969), and in Egypt (Gropp et al. 1969). According to Bhatnagar and El-Azawi (1978), the karyotype of *H. auritus* in Iraq consists of 43 macro- and 5 micro-chromosomes. We found the same karyotype in Turkish specimens, except the large metacentric X chromosome and the metacentric Y chromosome. The karyotype of *H. auritus* from Turkey is similar to that given by Zima and Kral (1984).

In *Erinaceus europaeus*, a karyotype of 2 n = 48 chromosomes has one medium-sized pair of acrocentric (Zima and Kral 1984), while there is no acrocentric chromosome in *H. auritus*. In most species of hedgehogs, the diploid chromosome number was described as being 48 (Geisler and Gropp 1967; Hsu and Benirschke 1968; Gropp et al. 1969; Natarajan and Gropp 1971; Gropp and Natarajan 1972). These authors noted large subtelocentric chromosomes in the karyotypes of other hedgehogs, as observed in the karyotype of *H. auritus* in Turkey. According to Doğramaci and Gündüz (1993), *E. concolor* in Turkey has 2 n = 48, NFa = 90 and NF = 94, the autosomes contain four pairs of large subtelocentric and one pair of small acrocentric, whereas acrocentric chromosomes are absent in the karyotype described in this study for *H. auritus*.

The sex chromosomes are variable in both *H. auritus* and the other hedgehogs. The X coromosome is metacentric (the smallest one of the macro-chromosomes) (Bhatnagar and El-Azawi 1978) and sub-metacentric (Hsu and Benirschke 1968) for *E. europaeus* and large metacentric (Doğramaci and Gündüz 1993) for *E. concolor*. We found the X chromosome to be large metacentric for *H. auritus*, which is different from that given by Bhatnagar and El-Azawi (1978), the same in *E. concolor* (Doğramaci and Gündüz 1993).

The Y chromosome is micro-chromosome and subtelocentric in *H. auritus* and a medium-sized submetacentric in *Paraechinus aethiopicus* (Bhatnagar and El-Azawi 1978), micro-submetacentric in *E. e. europaeus* and micro-metacentric in *E. concolor (*Doğramaci and Gündüz 1993). In *H. auritus* from Turkey the Y chromosome is micro-metacentric which is different from *H. auritus* from Iraq, *P. aethiopicus* from Iraq but similar to *E. concolor* from Turkey. This showed that the Y chromosome is variable in interpopulation as well as among intrapopulation in the family Erinaceidae.

Literature

Bhatnagar, A. N.; El-Azawi, T. F. (1978): A karyotype study of chromosomes of two species of hedgehogs, *Hemiechinus auritus* and *Paraechinus aethiopicus* (Insectivora: Mammalia). Cytologia **43**, 53–59.

Bobrinsky, N. A.; Kuznetsov, B. A.; Kuzyakin, A. P. (1965): Key to the Mammals of the USSR, 2nd ed. Moscow: Izdatel stvo. Prosveshchenie, (in Russian).

Corbet, G. B. (1978): The mammals of the Palaearctic Region: a toxonomic review. London and Ithaca: British Museum (Nat. Hist.). Cornel Univ. Press.

Corbet, G. B. (1988): The family Erinaceidae: a synthesis of its taxonomy, phylogeny, ecology, and zoogeography. Mammal Rev. **18**, 117–172.

Doğramaci, S.; Gündüz, I. (1993): Türkiye *Erinaceus concolor* (Mammalia: Insectivora) Türünün Taksonomisi ve Yayılışı. Doğa-Tr. J. Zoology **17**, 267–288.

Ellerman, J. R.; Morrison-Scott, T. C. S. (1951): Checklist of Palearctic and Indian Mammals 1758 to 1946. London: Brit. Mus. Nat. Hist.

Ford, C. E.; Hamerton, J. L. (1956): Colchicine-hypotonic citrate squash sequence for mammalian chromosomes. Stain Tech. **31**, 247–251.

Geisler, M.; Gropp, A. (1967): Chromosome polymorphism in the European hedgehog, *Erinaceus europaeus* (Insectivora). Nature **214**, 396.

Gropp, A.; Natarajan, A. T. (1972): Karyotype and heterochromatin pattern of the Algerian hedgehog. Cytogenetics **11**, 259–269.

Gropp, M.; Citoler, P.; Geisler, M. (1969): Karyotype variation and heterochromatin pattern in hedgehogs (*Erinaceus* and *Hemiechinus*). Chromosome **27**, 228–307.

Harrison, D. L. (1972): The Mammals of Arabia: Lagomorpha and Rodentia. Vol. 3. London: Ernest Benn. Pp. 385–670.

Harrison, D. L.; Bates, P. J. J. (1991): The Mammals of Arabia. Sec. ed. Kent: Harr. Zool. Museum. Pub.

Hondt, H. A. De (1972): Karyological studies on two insectivores of Egypt. Proc. Egypt. Acad. Sci. **25**, 171–174.

Hsu, T. C.; Benirschke, K. (1967): An atlas of mammalian chromosomes. Vol. 1. New York: Springer Verlag.

Natarajan, A. T.; Gropp, A. (1971): The meiotic behaviour of autosomal heterochromatin segments in hedgehogs. Chromosoma **35**, 143–152.

Niethammer, J. (1969): Zur Taxonomie der Ohrenigel in Afghanistan (Gattung *Hemiechinus*). Z. Säugetierkunde **34**, 257–274.

Orlov, V. N. (1969): Chromosome complements of the hedgehogs from East Europe. Mat. II. vsesoj. sov. pomlekopit. N. N. Voroncov (ed.): 6–7 (in Russian).

Osborn, D. J.; Helmy, I. (1980): The contemporary land mammals of Egypt (including Sinai). Fieldiana Zool. **5**, 1–579.

Schoenfeld, M.; Yom-Tov, V. (1985): The biology of two species of hedgehogs, *Erinaceus europaeus concolor* and *Hemiechinus auritus aegyptius*, in Israel. Mammalia **49**, 339–355.

Sobti, R. C.; Gill, S. S. (1980): Chromosome number in fifteen mammals from India. Mamm. Chrom. Newsl. **21**, 107.

Zima, J.; Kral, B. (1984): Karyotypes of European mammals I. Acta. Sc. Nat. Brno **8**, 15–17.

Authors addresses: Ercüment Çolak, Nuri Yiğit, and Mustafa Sözen, Department of Biology, University of Ankara, 06100 Beşevler/Ankara, Turkey; Şakir Özkurt, Department of Biology, University of Gazi, Kırşehir, Turkey.

Z. Säugetierkunde **62** (1997) 375–380

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Migratory behaviour of bats at south Swedish coasts

By I. AHLÉN

Department of Conservation Biology,
Swedish University of Agricultural Sciences,
Uppsala, Sweden

Receipt of Ms. 09. 12. 1996
Acceptance of Ms. 11. 03. 1997

From marking and recoveries, it has long been known that some bat species migrate between summer and winter haunts, e. g. *Myotis dasycneme*, *Myotis lucifugus* (e. g. EGSBAEK and JENSEN 1963; DAVIS and HITCHCOCK 1965). It has also been shown that some species undertake long distance seasonal north-south migrations, e. g. *Miniopterus schreibersi*, *Nyctalus noctula*, *Pipistrellus nathusii*, *Vespertilio murinus* in Europe and, e. g. *Tadarida brasiliensis*, *Myotis sodalis* in North America (AELLEN 1983; GRIFFIN 1970; MASING 1988, 1989; PETERSONS 1990; STRELKOV 1969; YALDEN and MORRIS 1975). It is also well known that bats are able to cross the sea since several species have been reported from many more or less remote islands, oil rigs and ships (BAAGØE and BLOCH 1994; PETERSEN 1994; STANSFIELD 1966). Among these records, migratory species prevail.

We know from marking that at least some bats on the Scandinavian peninsula are migratory (GERELL 1987). Two *Pipistrellus nathusii* marked in Skåne were recovered in Ger-

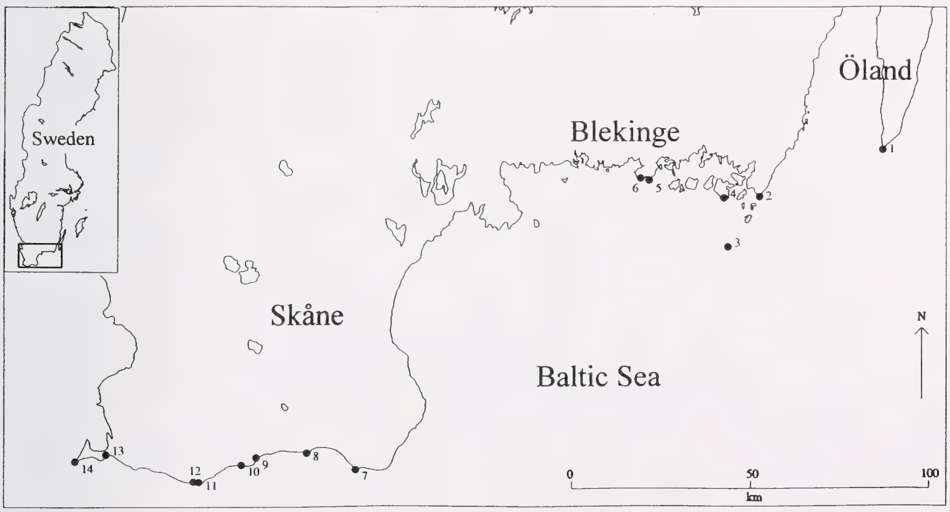


Fig. 1. Investigated sites at the south coasts of Öland, Blekinge, Skåne.
1. Ottenby (56°12′N, 12°24′E); 2. Torhamn; 3. Utklippan; 4. Uttorp; 5. Lindö; 6. Göudde; 7. Kåsehuvud; 8. Ystad, Revnäbbet; 9. Skivarpsån; 10. Hörte hamn; 11. Smygehuk; 12. Smygehuk light-house; 13. Falsterbo channel; 14. Falsterbo, Nabben (55°22′N, 12°49′E). Most observations on migratory behaviour were made in the period 25 August–10 September in 1993–1996. The local summer faunas were studied in July and early August.

many and Belgium. One *Nyctalus noctula* marked in Skåne was recovered in Germany. Because of the lack of a land connection to the continent in the south, these bats have to fly across the sea.

Data on regular bat migration across the sea, however, seem to be scarce or absent. The aim of this study was to investigate if it is possible to observe migrating bats by locating the sites where they leave land at the south Swedish coasts. This might be a first step in obtaining better knowledge of migratory behaviour.

A number of points and peninsulas along the south Swedish coasts of the provinces Skåne, Blekinge and Öland were selected from the map (Fig. 1). These localities were visited to find out whether there was any accumulation of bats or if any bats passing or leaving the shore actually could be observed.

The observation method was the use of ultrasound detectors (Pettersson Elektronik D-980, D-140, D-240) with tape recorder for documentation and subsequent analysis (Sony TCD-D7). Visual observations on flight behaviour and directions were possible with the aid of a strong 12 V halogen spot-light. Species identification was made according to methods described in AHLÉN (1981, 1990). When the bats had been discovered, mainly by the detector, they could often be followed over long distances with the visible light.

Unpublished data from the marking of bats at Pape bird station at the Baltic coast in south Latvia (PETERSONS 1990) were essential to find the right time of the year, namely when the peak number of bats was attained.

For four years, 1993–1996, the selected sites were visited during the time when migrating bats could be expected, mainly in late August and early September. Most of the sites were also visited during the non-migration period in the summer to investigate which species belonged to the local fauna of the nearby areas.

Increased bat activity with species not belonging to the local summer fauna occurred at almost all the studied sites. A total of 1 175 bats belonging to 12 different bat species was observed (Tab. 1). The species dominating in numbers was *Pipistrellus nathusii.* On some occasions, hundreds of this species were observed, while there were fewer representatives of all other species.

At two localities, Ottenby and Falsterbo, bats leaving land were observed (*Pipistrellus nathusii*, *Nyctalus noctula*, *Vespertilio murinus*) while no migration out over the sea was seen at any of the other coastal sites. At Kåsehuvud, a remarkable concentration of many bats of several species was found on two occasions but no migratory movement out over the sea was detected.

The following remarks on the observed bat species can be made:

Pipistrellus nathusii was the dominating species, despite being rare in Sweden, being observed at 10 of the 14 sites. At Ottenby, the approximate numbers observed accumulating and/or passing each night were (numbers of bats seen leaving land in brackets) 50, 30(3), 30, 3, 200, 250, 20, 30(30), 14(2), 4(1), 100(5), 1. At Falsterbo, numbers observed were 4(4), 5(5), 0, 0. During one night at Kåsehuvud, there were approximately 50 specimens in the area. The migrating bats observed at Ottenby arrived early in the evening, all of them following approximately the same route out over the sea at a height of only 2–3 m, with directions due south or a few degrees more to the west. On some evenings with strong winds, many bats accumulated over the open seashore (on the west side of the point) but took off when the wind-force fell. During gales, irrespective of wind direction, no bats appeared over the seashore. The migrating bats left land one by one, and no groups or flocks could be seen outside the aggregations over the shoreline. At Segerstad (north of Ottenby on the east coast of Öland), one bat was seen on 25 August 1996 in the morning by an ornithologist when it was coming in from the sea. The bat flew straight into a bird net and was identified as *Pipistrellus nathusii* (C. CEDERROTH, pers. comm.).

Pipistrellus pipistrellus. This species most often belonged to the local summer fauna but

Table 1. Bat observations at 14 sites. Total number of bats observed at each site (the maximum number observed on one occasion is given in brackets) and number of occasions when the species was observed. *Mm/b* = *Myotis mystacinus* or *brandti*, *Mnat* = *Myotis nattereri*, *Mdau* = *Myotis daubentoni*, *Vmur* = *Vespertilio murinus*, *Enil* = *Eptesicus nilssoni*, *Eser* = *Eptesicus serotinus*, *Nnoc* = *Nyctalus noctula*, *Nlei* = *Nyctalus leiseri*, *Ppip* = *Pipistrellus pipistrellus*, *Pnat* = *Pipistrellus nathusii*, *Bbar* = *Barbastella barbastellus*, *Paur* = *Plecotus auritus*.

	Mm/b	*Mnat*	*Mdau*	*Vmur*	*Enil*	*Eser*	*Nnoc*	*Nlei*	*Ppip*	*Pnat*	*Bbar*	*Paur*	No of spec.
Ottenby	2(1)2	2(2)1	26(20)4	1(10)2	17(4)8	1(1)1	13(10)4		97(20)10	703(250)12	2(2)1	1(1)1	11
Torhamn									20(20)1	4(4)1			2
Utklippan	6(6)1								1(1)1				1
Uttorp			1(1)1		5(5)1				20(20)1	5(5)1			5
Lindö		1(1)1							1(1)1				2
Göudde													0
Kåsehuvud				6(3)2	1(10)2		11(11)1	1(1)1	25(20)2	54(50)2			6
Ystad							2(1)2		28(23)3	2(2)2	2(2)1		4
Skivarpsån										1(1)1			1
Hörte hamn			10(10)1		4(2)3				4(3)2				3
Smygehuk				1(1)1	7(4)3		1(1)1		3(3)1	3(2)2			5
S. light-house				1(1)1	5(2)4		1(1)1		3(3)1	5(5)1			5
Falsterbo channel			2(2)1						5(5)1	5(3)2			3
Falsterbo				3(1)1	4(2)2		5(4)2		9(4)3	9(5)2			5
All sites, totals.	8	3	39	22	53	1	33	1	219	791	4	1	

occurred in large numbers and frequently flew out over the seashore. At Utklippan island (15 km from the mainland) one individual was found feeding there one evening in September. One specimen was also found dead in the grass on Utklippan on 12 May 1995 (G. STRÖMBERG, pers. comm.).

Nyctalus noctula was regular in small numbers at Ottenby, Falsterbo and Kåsehuvud with the maximum number of 11 specimens observed at Kåsehuvud, but was observed in small numbers at three other sites. Migrating specimens leaving land were observed at Falsterbo and Ottenby (one bat on each site). They left land early in the evening and flew much higher than *P. nathusii*, approximately 10 m above the water. The dates chosen for observations were not optimal for this species which probably has its migration peak somewhat later in the autumn. Some efforts to find this peak have failed so far. Large flocks of noctules flying in daylight in October have been reported from Skåne and some coastal areas more to the north. One noctule marked in Sweden was recovered in Germany. The species is definitely migratory within Sweden but is also known to hibernate in southern Sweden, so the extent to which Swedish noctules really leave the country is unknown (GERELL 1987, and pers. comm.). One specimen found hanging on a bush thorn at Utklippan, but still alive, was released on 27 May 1980 (G. STRÖMBERG, pers. comm.).

Nyctalus leisleri. One specimen was observed and recorded when hunting over the grass hills of Kåsehuvud on 30 August 1993. This was the first find of the species in Sweden. Most likely *N. leisleri* have been sited earlier at 3 or 4 localities in southern Skåne.

Vespertilio murinus was observed at Ottenby, Kåsehuvud, Smygehuk, and Falsterbo. On one evening at Ottenby two bats from a group of 5 were seen to fly away over the sea. At Falsterbo one specimen was observed leaving land in the evening. It flew at a height of about 10 m and disappeared in a southwesterly direction.

Myotis daubentoni was observed flying over the sea water surface at Ottenby, Uttorp, Hörte hamn, Smygehuk, and over the sea outside the Falsterbo channel. At least some of these bats were feeding and it was impossible to judge whether they were migratory or had just temporarily moved into the area for feeding.

Eptesicus nilssoni was observed regularly but in small numbers at almost all sites. At least at some sites the occurrence clearly exceeded what could be expected from nearby local fauna.

One specimen of *Eptesicus serotinus* was observed and recorded when flying around near the light-house at Ottenby on 27 August 1993. This was the first Swedish record of the species outside Skåne. Since then, in 1996, it has also been observed on northern Öland (AHLÉN 1997).

Two specimens of *Barbastella barbastellus* were observed and recorded when flying around the entire area, including the open seashore, at Ottenby on 6 September 1994. Two specimens were also observed at Ystad on 27 August 1996. In both cases the species did not belong to the local summer fauna.

This study showed that most of the selected sites at the south coast of Sweden had increased bat activity at the expected time of migration and dispersal. In some cases, real concentrations of many bats not belonging to the local summer fauna accumulated, swarming over the seashore. Bats actually leaving land and disappearing out over the sea were observed in three species. Altogether 12 bat species occurred at the selected sites which, at least to some extent, would be an expression of regional movements or migratory instinct in most of these species.

The remarkable accumulation of bats at Kåsehuvud can probably be explained by the shape of the coastline. Following the coast, the bats may find that the shore deviates too much from their innate migration direction there. It is also probable that the high south-facing slopes provide good feeding habitats for bats. The question is then if they, after some hesitation, continue along the coast or migrate across the sea at this site.

Thus, migrating bats leaving land for flights across the sea have been observed at Ot-

tenby and Falsterbo. It is, however, likely that bats leave land at more places somewhere between these two localities, e. g. Kåsehuvud. The bat *Pipistrellus nathusii*, which is the most numerous migrant observed in this study, has a flight speed of about 20 km/h (= 5.6 m/s) (Baagøe 1987). If they maintain the course they had when they left Ottenby, they would reach the Polish coast after flying 180 km for about 9 hours. When starting in the evening they will reach land the next morning in daylight. The distance to Bornholm is about 140 km (about 7 hours). However, the flight directions do not indicate that they are aiming for Bornholm. It is not even likely that the bats leaving Ottenby come to the coast of Blekinge, because only small numbers of bats have been observed at Torhamn and at Utklippan there are only a few records of bats but none of this species. There are a few direct observations reported to the author of bats coming in from the sea in spring, namely at Ottenby (C. Cederroth, pers. comm.) and at Torhamn (M. Jonasson, in lit.). In both cases, these bats came in full daylight, which would be expected with a departure time from the southern Baltic coast early the preceding evening.

Obviously, bats regularly migrate across the Baltic Sea from Öland and Falsterbo or other points along the coasts. This migration can certainly involve problems, as indicated by an observation reported from Skagen, the northernmost point of Denmark. Along a 200 m sandy shore about 10 dead bats were found on 16 September 1994, following several days with strong easterly winds (D. Nilsson according to M. Forslund, in lit.). The bats observed in spring at Torhamn and Ottenby were apparently exhausted, as was the bat found dead in the grass on Utklippan.

Pipistrellus nathusii is a rare species in Sweden. Apart from a few older records in southwestern Skåne published by Ryberg (1947), it has just recently been found in some areas in south and middle Sweden (Ahlén and Gerell 1990; Lundberg and Gerell 1994). Especially the number of bats observed at Ottenby, with hundreds of specimens accumulating and swarming at the shore, exceeds what could be expected from the known very small populations within Öland (Ahlén 1997). Could it be possible that these bats come in from the Baltic states, or are there still unknown populations in Sweden? *Pipistrellus nathusii*, marked and observed migrating at the Pape bird station in Latvia, follow the coast and have never been observed to migrate out over the sea (G. Petersons, pers. comm.). On the other hand, there is one observation from the east coast of Öland of a *Pipistrellus nathusii* coming in from the sea. The species has been able to colonize and establish a small population on Gotland (Ahlén 1983, 1994). Until further data on migration have been secured, the origin of bats passing Ottenby remains to be determined.

This study has shown that migratory behaviour in several species is indicated by accumulation of many bats at certain points of south Swedish coasts but also by direct observation of bats flying out over the sea. Some bats carry out long-distance migrations and regularly have to cross the Baltic Sea for up to about 9 hours' flight. There are clear indications, however, that this effort may be risky, namely the many bats obviously hesitating before departure and the exhausted or dead bats found at the seashores.

The occurrence of the 12 species indicates that the division in migratory and resident species is perhaps not so sharp. These observations, together with other observations recently made in Sweden, show that some of the most resident species also perform population movements between summer and winter habitats, perhaps much more than has been expected.

Acknowledgements

I am grateful to Mr. Gunnar Strömberg who made it possible for me to stay on the island Utklippan and to Mr. Jan Pettersson to stay at Ottenby bird station. Mr. Gunars Petersons allowed me to study unpublished data on bat migration at Pape in Latvia. Mr. Christian Cederroth, Mr. Mats Jonasson,

Mr. DAG NILSSON, and Mr. GUNNAR STRÖMBERG kindly reported their bat observations. I thank Dr. HANS BAAGØE, Copenhagen, Dr. RUNE GERELL, Lund, and Dr. JOHNNY DE JONG, Jönköping, for discussions about an earlier version of the manuscript.

References

AELLEN, V. (1983): Migrations de chauves-souris en Suisse. Bonn. Zool. Beitr. **34**, 3–27.

AHLÉN, I. (1981): Identification of Scandinavian bats by their sounds. Swedish University of Agricultural Sciences. Dept. of Wildlife Ecology, Report **6**, 1–56.

AHLÉN, I. (1983): The bat fauna of some isolated islands in Scandinavia. Oikos **41**, 352–358.

AHLÉN, I. (1990): Identification of Bats in Flight. Stockholm: Swedish Soc. Conserv. Nature.

AHLÉN, I.; GERELL, R. (1990): Distribution and status of bats in Sweden. In: European bat research 1978. Ed. by V. HÁNAK, I. HORÁCEK, and J. GAISLER. Praha: Charles Univ. Press. Pp. 319–325.

AHLÉN, I. (1994): Gotlands fladdermusfauna 1993. Visby: Länsstyrelsen i Gotlands län.

AHLÉN, I. (1997); Ölands fladdermusfauna. Kalmar: Länsstyrelsen i Kalmar län.

BAAGØE, H.(1987): The Scandinavian bat fauna: adaptive wing morphology and free flight in the field. In: Recent Advances in the Study of Bats. Ed. by M. B. FENTON, P. RACEY, and J. M. V. RAYNER. Cambridge: Univ. Press.

BAAGØE, H.; BLOCH, D. (1993): Bats (Chiroptera) in the Faroe Islands. Fróðskaparrit **41**, 83–88.

BARBOUR, R. W.; DAVIS, W. H. (1969): Bats of America. Kentucky, Lexington: Univ. Press.

DAVIS, W. H.; HITCHCOCK, H. B. (1965): Biology and migration of the bat *Myotis lucifugus* in New England. J. Mammalogy **46**, 296–313.

EGSBAEK, W.; JENSEN, B. (1963): Results of bat banding in Denmark. Vidensk. Medd. fra naturh. Foren. **125**, 269–296.

GERELL, R. (1987): Flyttar svenska fladdermöss? Fauna och flora **82**, 79–83.

GRIFFIN, D. R. (1970): Migration and homing in bats. In: Biology of Bats. Ed. by W. A. WIMSATT. Vol. I. New York, London: Academic Press. Pp. 233–264.

KOOPMAN, K. F.; GUDMUNDSSON, F. (1966): Bats in Iceland. American Museum Novitates **2262**, 1–6.

LUNDBERG, K.; GERELL, R. (1994): The mating behaviour of the pipistrelle and the Nathusius' pipistrelle (Chiroptera) – a comparison. Fol. Zool. **43**, 315–324.

MASING, M. (1988): Long-distance flights of *Pipistrellus nathusii* banded or recaptured in Estonia. Myotis **26**, 159–164.

MASING, M. (1989): A long-distance flight of *Vespertilio murinus* from Estonia. Myotis **27**, 147–150.

PETERSEN, Æ. (1994): Leðurblökur á Íslandi. Náttúru frædingurinn **64**, 3–12.

PETERSONS, G. (1990): Die Rauhhautfledermaus, *Pipistrellus nathusii* Keyserling u. Blasius, 1839), in Lettland: Vorkommen, Phänologie und Migration. Nyctalus (N. F.) **3**, 81–98.

RYBERG, O. (1947): Studies on bats and bat parasites. Stockholm: Svensk Natur.

STANSFIELD, G (1966): Parti-coloured bat *Vespertilio murinus* L. from a North Sea drilling rig. J. Zool. (London) **150**, 491–511.

STRELKOV, P. P. (1969): Migratory and stationary bats (Chiroptera) of the European part of the Soviet Union. Acta Zool. Cracoviensia **14**, 393–439.

YALDEN, B. W.; MORRIS, P. A. (1975): The Lives of Bats. Vancouver: David and Charles.

Author's address: Prof. Dr. INGEMAR AHLÉN, Department of Conservation Biology, Swedish University of Agricultural Sciences, P. O. Box 7002, S–75007 Uppsala, Sweden.

Z. Säugetierkunde 62 (1997) 381–382

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

MITTEILUNGEN DER GESELLSCHAFT

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 22. September 1997 im Hörsaal des Zoologischen Instituts der Universität Jena.

Der 1. Vorsitzende, Herr Erkert, eröffnet die Versammlung um 17.15 Uhr

1. Die Tagesordnung wird angenommen.
2. Herr Erkert verliest den Bericht über das Jahr 1996. Auf Einladung der Kollegen Dieter Kruska und Günter B. Hartl, Institut für Haustierkunde der Christian-Albrechts-Universität zu Kiel, fand die 70. Jahrestagung der Deutschen Gesellschaft für Säugetierkunde vom 22.–26. September 1996 in Kiel statt. Mit 33 Vorträgen und 10 Postern zu den Schwerpunktthemen „Evolution und Domestikation", „Populationsökologie" und „Säugetierschutz" sowie 12 Vorträgen und 24 Poster-Präsentationen zu freien Themen wurde den über 170 Teilnehmern ein interessantes und abwechslungsreiches wissenschaftliches Programm geboten. Dank finanzieller Unterstützung durch die DFG konnten erfreulicherweise auch einige namhafte ausländische Kolleginnen und Kollegen eingeladen werden. Auf der Exkursion konnten sich die Teilnehmer im Wikinger-Museum Haithabu über den wichtigen frühmittelalterlichen Fernhandelsplatz informieren und besuchten Schloß Gottorf sowie die eindrucksvolle Altstadt von Schleswig. Zur gleichen Zeit traf sich die „Koordinationsgruppe Feldermausschutz in Deutschland" zum Symposium „Ökologie und Schutz heimischer Fledermäuse" mit anschließender Exkursion zur Kalkberghöhle in Bad Segeberg. Bei der Führung durch das beeindruckende Höhlenlabyrinth wurden die Teilnehmer durch die Herren Alfred Orthmann und Stefan Lüders von der Ortsgruppe Bad Segeberg des „NABU" mit dem Schutzkonzept für dieses bedeutendste Fledermaus-Winterquartier Schleswig-Holsteins vertraut gemacht und konnten die dort von Herrn Kollegen Kugelschafter aufgebaute und demonstrierte High Tech Anlage zur automatischen Registrierung aus- und einfliegender Fledermäuse bewundern. Herr Erkert dankt den Veranstaltern, ihren Mitarbeiterinnen und Mitarbeitern und allen Organisationen für die Ausrichtung der gelungenen Tagung.

   Die Preise des Posterwettbewerbs der Kieler Tagung gingen an

   1. S. Münch und M. Braun, Freiburg/Karlsruhe: „Gibt es eine freilebende Skunkpopulation im Raum Freiburg/Breisgau?"
   2. C. Schmidt und N. Sachser, Münster: Futterverteilung, Verhalten und Streßhormonkonzentration von Breitmaulnashörnern (*Ceratotherium simum simum*) im Allwetterzoo Münster"
   3. K. Seluga und M. Stubbe, Halle: „Dichte, Verteilungsmuster und Besiedlungsstrategie von Feldhamstern (*Cricetus cricetus*) auf landwirtschaftlich genutzten Flächen im nordöstlichen Harzvorland".

   Die Zeitschrift für Säugetierkunde erschien in sechs Heften mit insgesamt 384 Seiten. Sie enthielt 38 größere Originalarbeiten, 10 wissenschaftliche Kurzmitteilungen sowie einige Mitteilungen der Gesellschaft und Buchbesprechungen. Den beiden Schriftleitern und den aktiven Herausgebern wird ebenso gedankt wie Frau Dr. Schlüter vom Fischer Verlag Jena.

Die Mitgliederzahl hatte sich bis Ende 1996 auf 596 verringert.

3. Herr ERKERT erläutert den von Frau KÜHNRICH abgefaßten detaillierten Kassenbericht und dankt der Schatzmeisterin für ihre sorgfältige und umfangreiche Arbeit.
4. Die Herren BOHLKEN und SCHLIEMANN haben die Kontounterlagen der Gesellschaft in Hamburg geprüft und für korrekt befunden.
5. Die Anträge auf Entlastung der Schatzmeisterin und des Vorstandes für das Geschäftsjahr 1996 werden bei 7 Enthaltungen angenommen.
6. Die Herren BOHLKEN und SCHLIEMANN werden als Kassenprüfer für das Jahr 1997 gewählt. Beide sind mit der Wahl einverstanden.
7. Der Vorstand schlägt vor, die Mitgliedsbeiträge für 1998 unverändert zu lassen. Dies wird einstimmig angenommen.
8. Die Mitgliederversammlung billigt einstimmig den Beschluß des Vorstandes, die 72. Jahrestagung vom 20.–25. September 1998 in Prag abzuhalten. Die Karls-Universität Prag hatte aus Anlaß ihrer 650-Jahrfeier dazu eingeladen. Als Schwerpunktthemen sind vorgesehen: „Monitoring und Diversität bei Säugetieren", „Morphologie der Säugetiere" sowie „Biologie der Insectivoren". Das Programm wird ergänzt durch einen festlichen Abend mit Konzert und eine Exkursion in den Zoologischen Garten von Dvůr Kralove.

Per Akklamation wird angenommen, daß Herr Dr. FLÖSSER, der Direktor des Pfalz-Museums für Naturkunde, für 1999 nach Bad Dürkheim eingeladen hat.

9. Die Tierschutzkommission hat bisher noch kein Positionspapier erarbeiten können. Das Positionspapier der Artenschutzkommission ist im Anschluß an die Kieler Tagung unter Berücksichtigung der Wünsche von Mitgliedern durch Herrn SCHRÖPFER bearbeitet und verschickt worden.
10. Herr GANSLOSSER berichtet, daß sich die Arbeitsgruppe „Tiergartenbiologie" vom 14.–16. November 1997 zum 5. Mal in Erlangen trifft. Herr NAGEL referiert über die Aktivitäten der Arbeitsgruppe für Fledermäuse, Herr SCHRÖPFER regt die Gründung einer Arbeitsgruppe zur Erforschung, Erhaltung und Wiederansiedlung des europäischen Netzes an. Interessenten werden gebeten, sich unmittelbar mit Herrn SCHRÖPFER in Verbindung zu setzen.
11. Herr SCHRÖPFER berichtet, daß eine Home page der DGS im Internet vorgesehen ist.

Die Sitzung endet um 18.50 Uhr

Prof. Dr. H. ERKERT 1. Vorsitzender	Prof. Dr. R. SCHRÖPFER Geschäftsführer	Dr. H. FRÄDRICH Schriftführer

Z. Säugetierkunde **62** (1997) 383–384

ZEITSCHRIFT FÜR SÄUGETIERKUNDE
INTERNATIONAL JOURNAL OF MAMMALIAN BIOLOGY

Buchbesprechungen

BARON, G.; STEPHAN, H.; FRAHM, H. D.: **Comparative Neurobiology in Chiroptera.** 3 vols. Basel, Boston, Berlin: Birkhäuser Verlag 1996. 1596 pp. DM 358,–. ISBN 3-7643-5394-5

In this three volume set the well-known brain researchers G. BARON (Montreal), H. STEPHAN (Frankfurt), and H. D. FRAHM (Düsseldorf) present a compilation on brain configuration, anatomy, size, and quantitative composition within the order Chiroptera from own data and results from the literature. This is a continuation of previously published comparative compilations on brains of Insectivora and Primates. Of the 925 chiropteran species described worldwide to date, 336 were treated here and 260 species of 149 genera were investigated in more detail and are documented in quantitative brain proportioning. Except for the families Myzopodidae (known in one species from Madagaskar) and Mystacinidae (one species distributed in New Zealand extant) all the other of the 18 families are represented by several or at least one species. Thus, an extremely large amount of species serves as a basis for a biological interpretation of brain size and composition, having resulted during evolutionary and adaptive radiation in this order.

The first volume mainly presents most of the raw data on macromorphology and brain composition in figures and tables. A short introduction is followed by a very detailed chapter on material and methods. Herein comments are made on the use of material from own collection and data from the literature, on several measurements, brain sectioning, determination of fresh-tissue volumes, calculations of species-specific standards, and on methods for comparison of brain size and volumes of structures. The most valuable effect of interspecific comparison lies in the consequent and critical utilization of the evaluating approach by means of the allometrical method on the basis of body size. Thus, as the authors performed earlier for the other orders, here also sizes of total brain as well as brains parts of Chiroptera are compared to those of the most primitive extant Insectivora, namely, the Tenrecinae. This resulted in body size-independent average encephalization or size indices for the species, genera, subfamilies, and families dealt with. The methodological comments are followed by a list of species sampled over four decades and used for brain sectioning in the laboratory of H. STEPHAN and another list of abbreviations for taxonomic units as well as for brain structures and other items used in all three volumes. Comparative brain characteristics are then described starting with macromorphology. These descriptions are visualized by very impressive outline drawings of brains from 16 representative species of Chiroptera in dorsal, lateral, and ventral views and by mediosagittal reconstructions of brains from 6 species. These figures give a general overview on the large diversity of brain shape and appearance within the order. The following two main chapters are devoted to comparisons. Encephalization indices and indices for brain parts are given and scaled for taxonomic groups as was usually performed by these authors in the past. Concerning total brain size, the Megachiroptera group (55 species) has reached higher encephalization indices between 226 (*Hypsignathus monstrosus*) and 404 (*Pteropus edwarsi*). Thus, they have brains about 2 to 4 times larger than Tenrecinae of comparable body size would have. The Microchiroptera (281 species) have lower indices from 83 (*Tylonycteris* spp.) to 312 (*Vampyros vittatus*). Bamboo bats thus have the smallest brains, even below the level of Tenrecinae. Telencephalon and diencephalon are distinctly larger in the Megachiroptera, whereas the indices for mesencephalon, cerebellum and medulla oblongata are about the same in both groups within a certain species-specific variation. In the following chapter 53 tables are given over 168 pages with original data on linear measurements, volumes, etc. and with calculated relative values resulting from these. The last chapter presents two atlases of several consecutive brain slices cut in the frontal plane together with corresponding drawings on opposite pages with markings of brain parts, regions, structures, nuclei, fibers and their delineations and boundaries. These are from a brain of *Rousettus amplexicaudatus* and *Myotis montivagus.*

The second volume contains two chapters of which one is focussed on brain characteristics in taxonomic units following the classification of CORBET and HILL (1980). This is a very critical, concise, and careful integration of what was published on general biology, brain, and sense organs of Chiroptera in the past. The other chapter concerned with size index profiles in taxonomic units discusses own results in more detail.

The third volume is concerned with the very diverse life styles of the Chiroptera. Brain characteristics are presented in connection with functional systems, ecoethological adaptations, adaptive radiation, and evolution. Thus, in one chapter physiological, histological, ethological and other results are discussed in connection with prominent brain structures of the olfactory, visual, somatosensory, auditory, vestibular, motor, and limbic system as well as with the neocortex in toto and with the primary areas. Another chapter is concerned with reflections on convergent major niche adaptations and especially discusses brain peculiarities of insect eaters, trawlers, gleaners, blood eaters, flower and nectar eaters, and fruit eaters. Finally the two last chapters are devoted to brain characteristics under the light of adaptive radiation and evolution and in connection with the monophyly-diphyly controversy of Mega- and Microchiroptera. Also here abundant information concerned with palaeontological data, comparative anatomy and other sources is debated, implying an independent and convergent evolution of flight, echolocation, and brain size in this order. References are listed on 169 pages at the end of the treatise and a subject index covering 26 pages.

The volumes are a unique and comprehensive compilation on brains of a special mammalian group and are valuable alone for the data sake as a source, but beyond this, the volumes are a highly valuable contribution especially with reference to their biological relevance.

D. Kruska, Kiel

Volf, J. (1996): **Das Urwildpferd, *Equus przewalskii.*** 4. überarbeitete Aufl. Die neue Brehm-Bücherei, Bd. 249. Magdeburg: Westarp Wissenschaften. 147 S., 89 Abb., 7 Tab. DM 39,90. ISBN 3-89432-471-6.

Wenn ein Buch in vierter Auflage erscheinen kann, wird deutlich, daß eine interessierte Leserschaft verfügbar ist. Es ist zu hoffen, daß dieses Interesse nicht nur ein Teil der „Pferdemode" ist, die überall auf der Welt zu beobachten ist, sondern hervorgerufen wird durch die Tatsache, daß ein in freier Wildbahn vermutlich ausgerottetes eindrucksvolles Säugetier in den letzten vierzig Jahren unter Obhut des Menschen eine mehr als vierzigfache Zunahme des Gesamtbestandes auf rund 1400 Tiere (1994) erfuhr.

J. Volf, 30 Jahre lang der Herausgeber des Internationalen Zuchtbuches für Przewalskipferde, schildert zunächst die Entdeckungsgeschichte des Urwildpferdes und erörtert seine Systematik und Nomenklatur. Die Erscheinungsform eiszeitlicher und heutiger Wildpferde werden dokumentiert, ferner werden Lebensweise und Verhalten in menschlicher Obhut geschildert. In einem eigenen Kapitel wir die Fortpflanzungsbiologie von *Equus przewalskii* behandelt. Aus eigener Erfahrung gibt J. Volf einen Einblick in die Organisation, sowie in die Führung und Verwaltung des Internationalen Zuchtbuchs für das Przewalskipferd. Dabei macht er besonders auf neue, Anfang der neunziger Jahres aufgetauchte Probleme aufmerksam: Dank der Zunahme der Individuenzahl können große Herden mit mehreren zeugungsfähigen Hengsten in großen Freiausläufen gehalten werden. Unter diesen Umständen können die Fohlen nicht mehr zweifelsfrei ihren Eltern zugeordnet werden. Der heutige Leiter des Zuchtbuches, E. Kûs, schildert weitere Probleme, wie sie sich aus der eigentlich höchst erfreulichen Bestandszunahme der Wildpferde ergeben: Inzuchteffekte aufgrund der langjährigen Gefangenschaftshaltung treten auf. Ferner bereitet die Ausbürgerung im ursprünglichen Verbreitungsgebiet in der Mongolei und in China finanzielle und organisatorische Probleme. Kompetenzrangeleien und die Anwesenheit von Hauspferden in den Auswilderungsgebieten von Przewalskipferden gefährden eine erfolgreiche Wiedereinbürgerung. Die Aridisierung weiter Gebiete im Südwesten der Mongolei, welche als wesentlicher Faktor für das Aussterben der Przewalskipferde in der freien Natur verantwortlich war, schreitet fort. Ein bis zum Jahre 1996 reichendes dreieinhalbseitiges Literaturverzeichnis und ein Stichwortregister schließen den vorliegenden Band ab.

P. Langer, Gießen

Instructions to Authors

Submission and Acceptance of Manuscripts: Manuscripts for publication should be sent to the managing editor, Prof. Dr. D. Kruska, Institut für Haustierkunde, Christian-Albrechts-Universität, Olshausenstr. 40–60, D-24118 Kiel, Germany, e-mail: dkruska@ifh.uni-kiel.de. Acceptance of the manuscript follows the bylaws of the German Society for Mammalogy (Deutsche Gesellschaft für Säugetierkunde). Receipt of the manuscript will be confirmed immediately by mail, and as soon as the peer reviews are received the authors will be informed concerning the decision for acceptance.

All correspondence dealing with details of production should be sent to: Zeitschrift für Säugetierkunde, Gustav Fischer Verlag, Villengang 2, D-07745 Jena, Germany.

Form of the Manuscript: Each manuscript should be submitted in triplicate, one original and two copies, in English or German in DIN A4 format either from a typewriter or legible computer print with a left-hand margin of 4 cm and true double spacing.

The first page of the manuscript should contain the following information:
title
name(s) of author(s): full first name for female authors, first initials only for male authors
department and university affiliation
In case of long titles, a running title not exceeding 72 characters should be provided.
Script type should be uniform throughout the manuscript. Use of bold print, italics and spaced-letters must be avoided.
Page footnotes and appendices at the end of the text are not allowed. Names of authors cited in the text are to be underlined in pencil. Botanical and zoological generic and species names should be underlined in pencil with a wavy line, whereby the name of the scientist who first described the species is not underlined.
Authors should indicate in the margins the approximate location in the text for illustrations and tables.
At the end of the manuscript following **References**, the exact postal address(es) of the author(s) should be given.

Content of the Manuscript: Manuscripts can be published as **original investigations** or **short communications.**

a) Original investigations: In addition to the text, original investigations should include illustrations, tables and references, and must not exceed 30 typewritten, double-spaced pages. The text should be divided into: Abstract (in English), Introduction, Material and methods, Results, Discussion (or together as Results and Discussion), Acknowledgements, Zusammenfassung (in German), References.

If written in German, an English title should precede the English abstract; if written in English, a German title should precede a German summary.

b) Short communications: Short communications must not exceed 5 typewritten, double-spaced pages and do not require either an Abstract or Summary. If written in German, an English title should be given on page 1; if written in English, please give a German title on page 1. Short communications need not be headed with subtitles into Introduction, Materials and methods, Results, and Discussion but should be organized according to this form.

Key words: Please supply five key words following the Abstract.

Illustrations: Number and size of illustrations must be kept to an absolute minimum. Only well focussed and readily reproducible original prints showing optimal contrast can be accepted; colour plates cannot be processed. Labelling on figures should be uniform, and large and clear enough for eventual reduction in size. On the back of each illustration the following information should be given, using a soft pencil: figure number, name of the journal, first author. Captions to figures should be written on a separate sheet of paper.

Tables: The number and size of tables must be reduced to a minimum. Each table should appear on a separate page including heading and running number.

Comprehensive tables not fitting onto one page should follow on consecutive DIN A4 format sheets of paper.

References: Each paper cited in the text must appear in alphabetical order at the end of the text. Only internationally available literature should be quoted. The names of the journals should be given in abbreviated form in conformity to international use.

Examples
a) From journals:
Kalko, E. K. V; Handley, C. O. Jr. (1994): Evolution, biogeography, and description of a new species of Fruit-eating bat, genus *Artibeus* Leach (1821), from Panamá. Z. Säugetierkunde **59**, 257–273.
b) From books:
Herre, W.; Röhrs, M. (1990): Haustiere – zoologisch gesehen. 2. Aufl. Stuttgart, New York: Gustav Fischer.
c) From reference books:
Niethammer, J. (1982): *Cricetus cricetus* (Linnaeus, 1758) – Hamster (Feldhamster). In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer und F. Krapp. Wiesbaden: Akad. Verlagsges. Vol. 2/I, 7–28.

Printing: The principal author will receive page proofs of the manuscript as well as a set of the illustrations and the original manuscript for proof reading. Only type-setting errors should be corrected. Any major revision undertaken by the author at this stage will result in costs to the authors themselves. The conventional proof-readers' symbols should be used. The corrected page proofs should be signed by the author to indicate that the paper is "ready for print" and be sent to Prof. Dr. Peter Langer, Institut für Anatomie und Zellbiologie, Justus-Liebig-Universität Giessen, Aulweg 123, D-35385 Giessen, Germany, e-mail: peter.langer@anatomie.med.uni-giessen.de

Reprints: 50 reprints of each paper are supplied free of charge. When returning the page proofs additional reprints can be ordered at the cost of the author(s).

Publisher: Gustav Fischer Verlag GmbH & Co. KG, Branch Office Jena, P. O. Box No. 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/6 26-3; Fax ++49(0)36 41/62 65 00; e-mail: office.j@gfischer.de
Advertisement bookings: Enquiries should be directed to Gustav Fischer Verlag, Advertising Manager: Sabine Schröter, P. O. Box 10 05 37, D-07705 Jena, Germany. Phone ++49(0)36 41/62 64 28, Fax ++49(0)36 41/62 64 21
Advertising rates: The price list from February 1, 1997 is effective at present.
Distribution and subscription agency:
For customers **in the German speaking countries:** Please turn to your bookshop or to SFG-Servicecenter Fachverlage GmbH, Zeitschriftenvertrieb: Barbara Dressler, Villengang 2, D-07745 Jena, Germany. Phone ++49(0)36 41/62 64 44, Fax ++49(0)36 41/62 64 43;
For customers **in all other countries:** Please contact your bookshop or Stockton Press., c/o Debbie Floyd, The Subscription Dept., Houndmills, Basingstoke, Hants RG 21 6XS, UK. Phone ++44(0)12 56/35 18 98. Fax ++44/12 56/32 83 39. Subscribers in the **USA** can call toll free on ++1/800/747 3187.
Terms of delivery (1997): 1 volume consisting of 6 issues.
Subscription rate (1997): Price per volume: DM 398.00; ÖS 2 906.00; sFr 382.50; UK Sterling 183.00
Single issue price: DM 80.00; ÖS 584.00; sFr 77.00; UK Sterling 35.00
STOCKTON
Reduced membership rates are available on request. Please turn to our publ. house.
All prices mentioned above are exclusive postage. USdollar prices are converted at the current exchange rate. We accept the following credit cards: VISA/Mastercard/American Express, (Please note card-No. and expiry date).
Banking connections:
For customers in the **German speaking countries:**
Deutsche Bank AG Jena, Konto-Nr. 6 284 707, BLZ 820 700 00.
For costumers **in the other countries:**
UK Post Office Giro Account No. 5 192 455. Full details must accompany the payment.
All prices are subject to change without notice.
Subsciption information: If not terminated the subscription will be effected until recalled. If no cancellation is given until October, 31st the delivery of the journal will be continued.

Type setting, printing and binding: druckhaus köthen GmbH
Printed in Germany

Printed on acid-free paper effective with vol. 61, no. 1, 1996.

New: For detailed journal information see our home page: http://www.gfischer.de

---

Abstracted/Indexed in
Animal Breeding Abstracts; Current Contents Agriculture, Biology Environmental Sciences; Biological Abstracts; *BIOSIS* database; Current Advances in Ecological and Environmental Sciences; Dairy Science Abstracts; Fisheries Review; Helminthological Abstracts; Index Veterinarius; South Pacific Periodicals Index; Veterinary Bulletin; Key Word Index to Wildlife Research; Wild Review (Fort Collins); Zoological Record